ANNUAL MEETING

February 1990 Volume 64, Number 1

NORTHWEST SCIENCE

CONTENTS

Announcements

1 Fertility Control in a Non-Native Population of Mountain Goats—**Roger A. Hoffman and R. Gerald Wright**

7 The Diet of Big Brown Bats (*Eptesicus fuscus*) in Relation to Insect Availability in Southern Alberta, Canada—**R. Mark Brigham and Matthew B. Saunders**

11 Browse Regrowth and Use by Moose After Fire in Interior Alaska—**James G. MacCracken and Leslie A. Viereck**

19 Habitat Use and Movement Patterns by Migrating Mule Deer in Southeastern Idaho—**Terry R. Thomas and Lynn R. Irby**

28 W-Waves and Plant Spacings—**O. E. Wagner**

39 The Effects of *Trichoderma* spp. Isolated from Burned and Non-Burned Forest Soils on the Growth and Development of *Armillaria* ostoyae in Culture—**Jimmy L. Reaves, Charles G. Shaw, III, and John E. Mayfield**

45 Causes of Basal Scars on *Chamaecyparis nootkatensis* in Southeast Alaska—**P. E. Hennon, E. M. Hansen, and C. G. Shaw, III**

55 Limnology, Vegetation, and Classification of Coast Range Slump-formed Ponds—**Bruce G. Marcot**

Volume 63 (1989) Author and Subject Index

Northwest Scientific Association

(Founded 1923)

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Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $14 per year ($8 per year for students). Institutional memberships, $40 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

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February 1990 Volume 64, Number 1

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Volume 63 (1989) Author and Subject Index

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In This Issue

As in the last issue of Volume 63, an annual dues renewal notice is included in this issue for the convenience of those members who have not yet renewed their membership. This form helps the Association to reduce the time and expense formerly spent on membership renewals. By completing it and returning it promptly with your annual dues your membership will be extended from its current expiration date.

—Editor

Annual Spring Meeting

The annual meeting of the Northwest Scientific Association will be held in the LaSells Steward Center at Oregon State University March 20-23. Yellowstone fires, Alaskan oil spill, earthquakes, and Mount St. Helens' eruption will be part of a symposium on "Environmental disasters: The nature of recovery."

Other features of the meeting include:

- The George Fahnestock Memorial Fire Science Symposium
- Mixing Science and Fun—A Wine and Cheese Social with an opportunity for students and researchers to meet
- Two interesting field trips
- A variety of half-day mini-symposia
- Award of student research grants
- Recognition of an outstanding Northwest scientist and the usual chance to hear your colleague's research results two years before they are published!

Remember, abstracts of all papers presented at the meeting are formally published as a supplemental issue of *Northwest Science.*

To students: We extend a special invitation and encourage you to give papers. Those who do will receive a free ticket to the NWSA banquet.

Spring comes early to the Willamette Valley which lies between the volcano-studded Cascades and the forest shrouded Coast Range. Plan your spring break to include a favorite winter or spring activity. Skiing is still fine at Mt. Bachelor, Mt. Hood, Hoodoo, or Willamette Pass. Grey whales are migrating along the coast, and waterfowl are abundant along the river and at wildlife refuges. A recent addition to Willamette Valley fun is an enthusiastic maturing wine industry, including vineyards and wine tasting rooms.

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Fertility Control in a Non-Native Population of Mountain Goats

Abstract

Because hunting and trapping are not always available to restrict overabundant wildlife populations, it is often necessary to find alternative methods of control. Our purpose in this study was to test the efficacy of two fertility control techniques on a non-native population of mountain goats in Olympic National Park, Washington. Females were treated with silastic implants containing megestrol acetate, males in a different population were chemically vasectomized. Reproductive success of treated females was reduced compared with untreated females in each year of study, and in over 40 goat years only 10 percent produced young. Although males were permanently sterilized as a result of this treatment, reproductive success of female goats within the same area was not affected. The tested procedures, while potentially effective in controlling the numbers of mountain goats, require capture of the animals to be treated and are therefore very expensive. These factors will probably limit widespread operational application of this technique. This method of control may however provide a valuable alternative in those situations where transplantation is not feasible and where policies or political factors hinder or prevent the use of lethal control methods.

Introduction

Overabundant or undesirable wildlife populations traditionally have been controlled through hunting and trapping. In many situations, however, these options are neither available nor desirable. For example, hunting and trapping are not acceptable techniques for population control in national parks. Animal welfare groups and the general public often object to any type of lethal control. Hence, more benign methods of population regulation must be sought. Such a situation exists with mountain goats (*Oreamnos americanus*) in Olympic National Park.

Although mountain goats are native to many mountainous areas of northwestern North America, the Olympic Peninsula was never colonized. About 12 mountain goats were introduced to the Olympic Mountains by local sportsmen between 1925 and 1929. Olympic National Park was established in 1938, encompassing most of the mountainous area of the Olympic Peninsula. The introduced mountain goat population flourished when afforded protection, and today over 1,000 mountain goats are present in the area (Houston *et al.* 1986a).

In addition to being a national park, Olympic is classified as a UNESCO Biosphere Reserve and World Heritage Site. These designations mandate that natural resources of the park be protected from negative influences. Mountain goats are a negative influence in the high country. They are changing the structure of endemic plant communities by grazing and trampling (Pfitsch 1981, Reid 1983), and increasing erosion around trails and wallows.

Olympic National Park has considered many techniques to control mountain goats including live-trapping, shooting, and fertility control. Other potential techniques were dismissed as impractical in the rugged terrain of the Olympic Mountains because of the danger posed to other animals or park personnel (Olympic National Park 1987).

Fertility control has been recognized as a wildlife management tool since the 1960s, but the technique has received relatively little attention. Sterilization is the only nonlethal population control alternative to transplantation. Sterilization techniques have been tested on a variety of animals including horses (*Equus caballus*) (Perkins *et al.* 1982, Wolfe 1982), asses (*E. assinus*) Carothers *et al.* 1976), white-tailed deer (*Odocoileus virginianus*) (Bell and Peterle 1975, Matschke 1977, 1980; Roughton 1979), cats (*Felis domesticus*) (McDonald 1980), coyotes (*Canis latrans*) (Stellflug *et al.* 1978), fox (*Vulpes vulpes*) (Linhart and Enders 1964, Allen 1982), skunks (*Mephitis mephitis*) (Storm and Sanderson 1969), other predators (Balser 1964), and black-tailed prairie dogs (*Cynomys ludovicianus*) (Garrett and Franklin 1983). Results, although mixed, show a potential that warrants further investigation. Research on sterilization has been hampered by high costs associated with the development and licensing of drugs and the difficulty of treatment application in wild populations.

[1]Present Address: Olympic National Park, 600 E. Park Ave., Port Angeles, Washington 98362

Female hormone implants appear to be the most effective and efficient technique tested (Matschke 1980). Two widely tested compounds for female implants are diethylstilbestrol (DES) and megestrol acetate (MGA). DES is a synthetic estrogen that interferes with implantation or causes early embryonic death. DES has been used successfully to control reproduction in coyotes (Balser 1964, Stellflug *et al.* 1978). MGA is widely used in cattle and sheep; it is safe for either sex and all ages, and it has no undesirable side effects.

One potentially useful technique for male sterilization is chemical vasectomy or epididymectomy. Injection of sclerosing agents (acetic acid, zinc tannate, lactic acid, formaldehyde, etc.) into the testis (Fahim *et al.* 1982) epididymis (Pineda and Hepler 1981, Pineda and Dooley 1984, Barnett 1985) or vas deferens (Pineda 1978) results in permanent sterility of the male. Barnett (1985) reported azoospermia in nine of nine treated dogs within 35 days of treatment; similar results were achieved by others using this technique on various species. This technique does not affect behavior of the male. It is also safe; hemorrhage is unlikely and infection is less likely than with surgical techniques, especially under field conditions. No surgical equipment is needed and little training is necessary to carry out the procedure.

This study tested two fertility control techniques on mountain goats. It was designed to test whether these techniques could be employed in an operational program to reduce mountain goat numbers in the park. These techniques are new and their use in free-ranging wildlife species has been limited.

Study Area

The study covered mountain goat populations inhabiting mountainous portions of Olympic National Park, located at the center of the 10,400 km^2 Olympic Peninsula in northwest Washington. The Olympic Mountains are dominated by Mount Olympus at 2,428 m. Glaciation and stream erosion have produced 10-11 major drainages radiating in a spiral towards the lowlands and the coasts of the Pacific Ocean and Strait of Juan de Fuca. The climate is maritime. Winters are mild and wet; summers are cool and dry. The mountains form an abrupt barrier to moist, westerly winds off the Pacific Ocean, causing a steep west to east gradient in precipitation. Average annual rainfall ranges from 400-500 cm along western windward slopes to 46 cm along northeastern leeward slopes. Mixed coniferous forests dominated by Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*) or western hemlock (*Tsuga heterophylla*) are found throughout the low and middle elevations. Forests above 550 m are dominated by Pacific silver fir (*Abies amabilis*), mountain hemlock (*Tsuga mertensiana*), and subalpine fir (*Abies lasiocarpa*). Herbaceous plant communities at high elevations are diverse. They range from moist subalpine meadows dominated by red mountain-heather (*Phyllodoce empetriformis*) and black alpine sedge (*Carex nigricans*) to scattered plants on drier scree slopes.

Methods

Capture and Treatment of Females

Five females were captured by darting from a Hughes 500D helicopter using Palmer cap-chur darts (3 cc) fitted with plastic tails (Simmons) and 3.1 cm barbed needles. Needle barbs were trimmed to reduce injury to the animals. A Gerwig® variable-range capture rifle was used to deliver 3 cc of carfentanil citrate (an experimental tranquilizer), M99 (etorphine hydrochloride), or a mixture of the two into animals. After capture, the animal was given an intravenous (where possible) 3-4.5 cc dose of 2 mg/cc diprenorphine hydrochloride (M50-50) as an antagonist to the tranquilizer.

Four female goats were captured with foot snares and three females were drive-netted. The foot-snare technique was used extensively in previous studies of mountain goats in the Olympics (Stevens 1983) and required a salt-source as bait and simple rope snares that were operated manually. Drive-netting used 2.4 m high nets 25 m in length and a helicopter to chase mountain goats into the netting.

Initially, an attempt was made to select female goats from widely separated populations for these treatments. After animals from four widely separated areas were treated, however, it became apparent that logistical difficulties in monitoring these animals were too great. The remainder of treated females were captured from a smaller area to simplify monitoring.

Cylindrical silastic implants 13 mm in diameter and 40-50 mm in length containing from 4.53 g to 6.46 g of MGA were surgically placed subdermally in the neck region of captured females. Treated goats were fitted with radio collars to facilitate relocation.

Capture and Treatment of Males

Male mountain goats selected for treatment inhabited an area approximately 3 km from the area inhabited by most treated females. Although there was some risk that animals from one area might disperse into the other, economic and logistical advantages outweighed these concerns. Population data also were available on mountain goats in this area (Houston *et al.* 1986a).

We tried to choose the largest males to ensure social dominance and therefore, reproductive potential. Five male mountain goats were captured by aerial darting. These captures and treatments were accomplished more than three months prior to rut to allow enough time for complete sterility to occur. These animals were sterilized by injecting 0.75 cc Chemcast® (Bio-Ceutic Laboratories, Inc. Div. of Philips Roxan, Inc., St. Joseph, Missouri 64502) into the caudal epididymis of each testis. Chem-cast is a sclerosing agent consisting of 88 percent lactic acid and 12 percent inert ingredients. This substance, and those of similar pharmacology, have rendered males of many different species permanently sterile when injected into the testis (Fahim *et al.* 1982, Barnett 1985) or the vas deferens (Freeman and Coffey 1973). By sclerosing the caudal epididymis, the passage of sperm from the testis should be blocked without affecting hormonal levels and associated behavior patterns.

The caudal epididymis was chosen for the ease with which it could be isolated in the field. This facilitated injection of the solution without penetrating the testis or the nerves and blood vessels associated with the caput area of the epididymis. Treatment of each testicle was done with multiple injections from a single insertion of the needle, accomplished by changing the depth and angle of the needle for each injection. This procedure ensured that many areas of the epididymis were treated so as to completely block sperm. To determine the success of the treatment, reproductive organs of four treated males were collected two years after treatment and compared with those of four untreated males.

Censuses of Males and Females

The Appleton Pass and Mt. Carrie subpopulations were censused by helicopter both in 1985 and 1986 to evaluate the effects of the treatments. The methods used are as described by Houston *et al.* (1986a). In addition to the census, an index of sightability was determined using techniques refined by Samuel (1984). The study areas were first censused using only visual cues to locate mountain goats. When a mountain goat wearing a radio-collar was located, its identity was established either through visual inspection of ear tag numbers or by using a radio telemetry receiver. After the census was completed, the receiver was again turned on and the remaining radio-collared goats in the area were located. Thus, the efficiency of the census could be evaluated by comparing the number of radio-collared goats detected during the census with the number actually known to be in the area. This efficiency was used to 'adjust' counts of detected animals to estimates of total numbers in the censused area. Treatment effectiveness of females was tested with a *Z*-test (Zar 1984:395-397) comparing the proportion of females seen with young in treatment and control groups.

Results

Females

Each of the 11 female mountain goats given MGA implants in 1982, 1983, and 1984 was relocated annually through 1987 to determine its reproductive status (Table 1). At present, the effective life of the MGA implants is still uncertain; preliminary results suggest that the life expectancy of the implants is at least four years and could exceed five years.

In 40 goat-years of observations on treated females, four kids were produced yielding a 10 percent rate of kidding. The rate observed in non-treated females was 68 percent (47/69) over 69 goat-years (Table 2). The reproductive rate of treated females was significantly lower ($P < 0.005$) than that for untreated females during each year of the study.

Males

One of the five males treated was killed in an avalanche. Two of the remaining four males stayed with the censused sub-population of

TABLE 1. Number of young produced by MGA treated female mountain goats in Olympic National Park, Washington 1983-1987.

Tag No	1983	1984	Year 1985	1986	1987
11[a]	0	0	0	0	0
12[a]	0	0	0	0	0
2[b,d]		0	0	0	0
3[b]		0	1	0	0
4[b,d]		0	0	0	0
5[b]		0	0	0	1
6[b,d]		0	0	0	0
7[c,d]			0	0	0
8[c,d]			0	1	0
9[c]			1	0	0
10[c]			0	(dead)	—
Reproductive Success	0/2	0/7	2/11	1/10	1/10

a) treated in 1982 b) treated in 1983 c) treated in 1984 d) females known to have bred successfully prior to treatment. (Reproductive history of the other females was unknown.)

TABLE 2. Comparison of reproductive rates for treatment and control groups of female mountain goats in Olympic National Park, 1983-1986.

Year	Treatment Group	Control Group	Z[a]	Z*[b]	P(Z*)
1983	0/2	3/4	1.732	2.598	0.0047
1984	0/7	7/13	2.408	2.900	0.0019
1985	2/11	20/26	3.326	3.718	0.0001
1986	1/10	17/26	2.977	3.349	0.0004
1987	1/10	—	—	—	—

a) one-tailed test b) correction for continuity

females during the rut, whereas the two remaining treated males dispersed upwards of 11 km to other areas of the park. All four treated males apparently participated in the rut, as evidenced by their close association with females and dark stains on their flanks. Staining is associated with the digging of rutting pits (Geist 1964, Chadwick 1973, Hoffman pers. obs.). Comparative examination of the reproductive organs from the four treated males indicated that the caudal epididymis of each was blocked and thus the males were effectively sterilized. As shown in Table 3, aerial censuses in the area occupied by the males indicated no change in population size or reproductive rates between 1985-1986.

TABLE 3. Comparison of population size and reproductive rates for Mt. Carrie during 1985 and 1986. Data are from helicopter censuses.

Year	Date	Estimated Population[1]	Kid/Nanny	Kid/Adult
1985	6 Aug	29	0.50	0.25
1986	23 July	28	0.80	0.27

[1]Corrected for sightability (71%)

Discussion

Females

The MGA implants were effective in reducing reproductive performance of female mountain goats. The data suggest an effective period of at least four years with 90 percent effectiveness. The maximum length of the effective period is undetermined. Predicted life-expectancy of cylindrical MGA implants was three years; however, recent findings from other species suggest this might be a conservative estimate (U.S. Seal, V. A. Medical Center, Minneapolis, MN., pers. commun.). Changes in the geometry of the implant may allow this period to be extended. These changes are based upon the relationship between surface area of an implant and diffusion rate of steroids through the silicone rubber. Implants with relatively small surface areas have lower rates of diffusion and can be expected to have a long effective life (Dziuk and Cook 1966).

Over the course of the study, 90 percent of the treated females were without offspring in early spring. This may not be a true indicator of the effectiveness of hormone implants because neonatal mortality cannot be ruled out. Using techniques described by Sasser *et al.* (1986), blood samples from ruminant females can be assayed for pregnancy/specific protein B (PSPB). Presence of PSPB suggests current or recent pregnancy. This technique has been tested in mountain goats, mule deer and white-tailed deer and found to be a reliable test of pregnancy (Houston *et al.* 1986b, Wood *et al.* 1986). Blood samples obtained prior to or shortly after the normal parturition period would provide a better test of the efficacy of MGA implants but would require recapture of females each year.

Males

Although the four males were effectively sterile and participated in the rut, they apparently had

no effect on reproduction or population size in the study area. The fact that less than 50 percent of the males in the subpopulation were treated may have influenced this outcome. The extended movement of two of the treated males out of the study area and the possible movement of untreated males into the area may also have contributed to the inability to show treatment effects. Likewise, interpretation of mountain goat breeding behavior could also be incorrect, multiple inseminations may occur more frequently than believed. Despite these problems, this technique may have potential in managing the mountain goat population if a larger number of animals can be treated and if the selected large goats do dominate breeding.

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Acknowledgments

We appreciate the invaluable assistance of R. Olson, B. Moorhead, P. Crawford and others at Olympic National Park. J. Mott, Eagle Air Helicopters piloted the aircraft used in the captures and telemetry. U. S. Seal provided implants. R. G. Sasser and D. B. Houston reviewed an early version of this paper. Funding was provided by the National Park Service through the Cooperative Park Studies Unit at the University of Idaho (subagreement no. 5 to CA-9000-3-0002). Olympic National Park provided essential financial and logistical support. This paper is contribution number 490 of the University of Idaho, Forestry and Wildlife Resources Experiment Station.

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Received 6 June 1989
Accepted for publication 13 November 1989

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The Diet of Big Brown Bats (*Eptesicus fuscus*) in Relation to Insect Availability in Southern Alberta, Canada

Abstract

The purpose of this study was to determine if bats preferentially select certain prey types by comparing the diet of big brown bats (*Eptesicus fuscus*) with insect samples collected at the sites where the bats were captured. We analyzed 135 fecal pellets collected from 14 bats captured in Writing-On-Stone Provincial Park, near Milk River, Alberta, Canada (49° 05'N, 111° 37'W). We used a combination of sticky, Malaise, and whirligig traps to sample the insect prey available to the bats. Despite the predominance of dipterans in insect trap samples, more than 65 percent of the diet of *E. fuscus* consisted of coleopterans even though beetles constituted less than 2 percent of the insects in the trap samples. Less than 10 percent of the bat's diet consisted of dipterans. We conclude that although our sampling methods were biased, foraging by *E. fuscus,* although probably selective, is flexible, and can vary with the size and type of prey available.

Introduction

Our present knowledge of the foraging behaviour of most species of insectivorous bats does not allow us to answer the question, "Do individuals preferentially select different prey types?" Prey selection could reflect any combination of energetic considerations predicted by optimal foraging theory (Stephens and Krebs 1986), detection constraints imposed by echolocation call design (Barclay 1985), limitations on habitat use determined by wing morphology and flight style (Norberg and Rayner 1987, Aldridge and Rautenbach 1987), or diet variation as a result of differences in prey availability between sites. To further our understanding of prey selection by bats, diet data for the same bat species from different locations and measures of prey availability in those locations are needed.

In this paper we present data on the diet of big brown bats (*Eptesicus fuscus*) from southern Alberta, and we compare bat diet with the availability of insect prey measured at the same site. The diet of *E. fuscus* has been reported from a number of localities in North America (Hamilton 1933; Ross 1967; Whitaker 1972; Black 1972, 1974; Whitaker *et al.* 1977, 1981), but in only one instance has diet of this species and prey availability been measured simultaneously (Brigham 1988).

Study Area

Fecal pellets and insect samples were collected from bats caught in or near Writing-On-Stone Provincial Park near Milk River, Alberta (49° 05'N, 111° 37'W). The Park spans the Milk River valley and includes parts of several major coulee systems. The area is centered in Alberta's semi-arid, mixed grassland region, and is characterized by low precipitation, low humidity, strong winds and hot summers. The main river valley is flanked on both sides by steep sandstone cliffs and hoodoo formations. A variety of habitats including riparian (dominated by western cottonwood (*Populus deltoides*)), coulee and upland are present (Saunders 1989).

Materials and Methods

Fourteen bats were captured in mist nets on six nights during June and July, 1988. The bats, captured as they foraged in coulee systems adjacent to the Milk River, were kept in cotton bags for a minimum of one hour after which fecal samples were collected. Most feces are voided during the first hour after capture (Warner 1985). We determined the diet for 13 individuals using 10 pellets randomly selected from each bat's feces. One individual produced only five pellets, all of which were analyzed. For each pellet examined, we estimated the percentage volume of each identifiable insect Order with a 6x to 30x dissecting microscope. The frequency of occurrence in the diet was defined as the percentage of pellets in which an insect Order was found.

Insect abundance was measured on five of the six nights that bats were captured. We used one or more traps or trap types on any given night. These included three sticky traps, two Malaise traps and a whirligig trap (Kunz 1988). We used

these different traps because of their availability to us and the nature of the sampling sites. The whirligig trap was dependent on a source of electricity and could not be used in remote locations. All insect traps were placed within 100 m of the nets used to capture the bats. The sticky traps were hung 0.5, 1.0 and 1.5 m from the ground and the Malaise traps were placed on the ground. The nets on the whirligig trap sampled insects flying at 0.5 and 3.5 m from the ground. We observed the bats feeding at dusk in the area of nets and insect traps, but it was impossible to determine what proportion of their total foraging time was spent in the area. Brigham (1988) and Brigham and Fenton (1986) showed that the range of foraging sites used on a given night by radio-tagged *E. fuscus* may be concentrated at a single predictable location or scattered among numerous unpredictable locations. Therefore, we do not know if the bats foraged near the traps in our study area for the whole night on a regular basis or for only a short period of time on an irregular basis.

To estimate the relative abundance of each insect Order, we summed the number of individual insects of each Order caught by the traps on a given night.

Results

The results of the diet analysis show that coleopterans dominated the diet of *E. fuscus* in terms of both volume and frequency (Table 1), despite the fact that only 1.9 percent of the insects captured in the traps were beetles (Table 2). Lepidopterans (moths) and hemipterans (bugs) were the only other insect Orders contributing more than 10 percent to the dietary volume during the dates we sampled. Dipterans (flies) constituted 79.3 percent of the insects captured by the traps, but made up only 7.7 percent of the volume of the diet of *E. fuscus*. No other insect Order constituted more than 10 percent of the trap samples.

Using the same method of analysis as Swift *et al.* (1985) we found no significant correlation between prey availability and diet on any of the four nights when insects were caught (Spearman rank $r_s = 0.21$, -0.42, -0.48, and -0.40 for 20 June, 7 July, 16 July and 25 July respectively; $p > 0.05$ in each case). These results indicate that the diet composition of *E. fuscus* does not reflect insect availability as measured by our traps, but suggests either selective feeding by the bats or differential vulnerability of prey types to capture.

Discussion

Our results concur with the findings of Hamilton (1933), Ross (1967), and Whitaker (1972) in suggesting that beetles are the most important dietary item in this species. Potential beetle preference is reinforced by the results of our insect sampling as beetles were relatively rare in our traps (although see below). In contrast, however, in the two localities closest to our study area where the diet of *E. fuscus* has been described, the predominate prey items were moths (Whitaker *et al.* 1977) and caddisflies respectively (Brigham 1988). Together, these data indicate that labelling *E. fuscus* as a beetle strategist (sensu Black 1974) is inappropriate. We suggest this species would be better described as being

TABLE 1. Summary of percent frequency (F) and volume (V) of insect Orders found in the diet of *Eptesicus fuscus*. Lep. represents lepidopterans; Col. coleopterans; Hem. hemipterans; Dip. dipterans; and Tri. trichopterans.

		Lep.		Col.		Hem.		Dip.		Tri.		other	
Date	# bats	F	V	F	V	F	V	F	V	F	V	F	V
2 June	4	65.7	45.4	54.2	32.8	2.8	0.3	40.0	20.3	0.0	0.0	8.6	1.1
20 June	4	12.5	6.5	77.5	61.5	37.5	25.4	10.0	6.0	2.5	0.2	0.0	0.0
7 July	2	0.0	0.0	100	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16 July	1	0.0	0.0	100	97.0	0.0	0.0	0.0	0.0	10.0	3.0	0.0	0.0
25 July	1	40.0	16.0	40.0	25.0	80.0	55.0	10.0	2.0	0.0	0.0	10.0	2.0
31 July	2	5.0	1.0	30.0	26.0	75.0	70.0	5.0	3.0	0.0	0.0	0.0	0.0
total	14	24.4	15.1	66.6	54.5	28.9	22.1	14.8	7.7	1.5	0.2	3.0	0.4

TABLE 2. Summary of the number of each insect Order found in trap samples. Insect Order abbreviations are the same as in Table 1.

Date	trap	Lep	Col	Hem	Dip	Tri	other
2 June	sticky	0	0	0	0	0	0
20 June	sticky	4	1	0	1	1	0
7 July	sticky	3	0	0	13	0	2
	Malaise	1	0	0	13	0	3
16 July	sticky	2	0	0	7	0	0
	Malaise	0	0	0	2	0	0
25 July	sticky	2	0	0	14	0	4
	w-gig	11	4	0	157	1	15
Total	number	23	5	0	207	2	24
	percent	8.8	1.9	0.0	79.3	0.8	9.2

capable of eating hard-bodied insects such as beetles (e.g., Freeman 1981), although not restricted to eating them.

In both this study and that of Brigham (1988), *E. fuscus* did not select prey relative to availability. Brigham (1988) found that *E. fuscus* did not eat chironomids (midges), despite these being the most abundant insect at his study site. Small insects such as chironomids or dipterans may not be available as a result of detection constraints for *E. fuscus* (Barclay 1985). It is likely that the predominance of caddisflies (body length $>$ 5 mm) in the diet of *E. fuscus* in Brigham's (1988) study reflected the fact that they were the only relatively large insect regularly available.

Our data are more difficult to interpret. Saunders (1989) found that both *Myotis lucifugus* and *M. volans,* sympatric with *E. fuscus* at Milk River, ate both dipterans and lepidopterans. The diet of these species was much more in accordance with the insect availability measures than our data for *E. fuscus.* Saunders (1989) found that dipterans caught in the whirligig trap were relatively small (2 mm), but the moths were generally larger than 10 mm in body length. If prey size, and hence detectability, influences prey selection by bats, the limited selection of flies is explained. However, if prey size is the only important criteria, we would have expected moths to constitute a greater proportion of the diet of *E. fuscus* than did the coleopterans.

Although a variety of different traps have been designed to collect insects, our results illustrate the biases inherent in all insect sampling devices (Southwood 1978, Kunz 1988). Most traps are either prone to catching certain insect types, or have limited success in catching large or fast-flying insects. Graham (1969) concluded that whirligig traps generally take a random sample except for mosquitoes which are attracted, while Juillet (1963) found that these traps caught few large beetles. Juillet (1963) showed that Malaise traps caught relatively few insects and were biased against catching coleopterans and hemipterans. Heathcote (1957) found that sticky trap shape was also important, with cylindrical traps like those used in our study being the most efficient. However, since sticky traps partly make use of wind to catch insects, the airflow pattern at the sampling site can greatly influence sampling efficiency. Juillet (1963) found that sticky traps catch smaller insects than Malaise traps and that they are inefficient at catching large insects. He concluded that of the three types, whirligig traps were the least biased. This agrees with Saunders (1989), who suggested that the whirligig trap caught the most representative sample of insects available to foraging bats. As noted however, the drawback to this trap is the need for a power source. Swift *et al.* (1985) used a suction trap which is also relatively unbiased (Southwood 1978), but also requires a source of power (Kunz 1988). We suggest that future studies concurrently measuring diet and prey availability should use more than one type of insect sampling device, preferably including a whirligig or suction trap which seem to collect the most representative samples.

It is almost certain that our sampling methods (especially the sticky and Malaise traps) underestimated the actual availability of the large, strong flying coleopterans eaten by *E. fuscus* and were biased toward the smaller, weaker flying dipterans. However, even after accounting for the sampling problems, our results, when compared with Brigham's (1988) data where insects were sampled using only a whirligig trap (the same trap as in this study), suggest that prey availability can influence selection by *E. fuscus.* Even our whirligig trap rarely caught beetles, which were the preferred prey type of *E. fuscus.* We conclude, therefore, that foraging by this species, although probably selective, is flexible, and can vary with the size and type of prey available.

Acknowledgments

This study was supported by an Alberta Recreation, Parks and Wildlife Foundation grant to M. B. Saunders and R. M. R. Barclay, Natural Sciences and Engineering Research Council (NSERC) grants to R. M. R. Barclay and an NSERC postdoctoral fellowship to R. M. Brigham. We thank G. L. Holroyd for the loan of the whirligig trap and H. L. Sims for her help. A. C. Brigham, R. L. Mackey, and C. E. Koehler read and commented on earlier versions of the manuscript.

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Received 20 February 1989
Accepted for publication 1 November 1989

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Browse Regrowth and Use by Moose After Fire in Interior Alaska

Abstract

This study was undertaken to estimate the short-term effects of fire on plant response and moose (*Alces alces* Miller) browse following the Rosie Creek fire near Fairbanks, Alaska. The fire consumed forests of quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and white and black spruce (*Picea glauca* (Moench) Voss, *P. mariana* (Mill.) B.S.P.). The fire began in late May 1983, was hot and fast moving, and burned over 3,000 ha. Browse regrowth was abundant within two months. Regrowth was from root and stump sprouting of quaking aspen, paper birch, and willows (*Salix* spp.). Generally, aspen sites produced the most browse followed by white spruce, birch, and black spruce. Composition of the pre-fire plant community, which was directly related to stand age, strongly influenced browse regrowth. Seedling establishment of browse species was evident by the third growing season after the fire. Moose foraged in the burn the first winter after the fire. Browse use ranged from 1 to 46 percent and was greatest on willows. Estimates of browse use based on stem counts and biomass data were significantly correlated. Crude protein and mineral concentrations differed among browse species and decreased as time after the fire increased. This suggests that wildfire can have immediate benefits to moose by the production of substantial browse within a few months.

Introduction

Moose (*Alces alces* Miller) in Alaska are associated with habitats in early stages of plant succession (LeResche *et al.* 1974). These plant communities provide significant amounts of deciduous hardwood browse on which moose feed (LeResche and Davis 1973, Cushwa and Coady 1976). Fire is currently, and was historically, the most significant force creating early seral vegetation communities in interior Alaska (Viereck 1973).

Burning of old-growth forests leads to increases in the quantity and quality of moose browse (Oldemeyer 1974, Oldemeyer *et al.* 1977). Browse regrowth after fire is from root and stump sprouting, or from seed. Sprouting can result in extremely dense stands (Spencer and Hakala 1964, Wolff and Zasada 1979). Fire in old-growth stands results in a release of nutrients from slowly decomposing organic matter and from soil layers with permafrost (Viereck 1973). Increased quality of browse, however, may be related more to greater digestibility of younger plants than to increased nutrient concentrations in plants (Oldemeyer 1974, Irwin 1985).

The amount, species, and quality of browse regrowth after fire depends on several factors. The composition of the pre-fire plant community, which is often related to stand age, strongly influences species composition of burned sites. Time of year that a fire occurs is also important, as is fire intensity, size, and burn patterns (Viereck 1973, LeResche *et al.* 1974, Gasaway and Dubois 1985).

Land managers in interior Alaska are incorporating controlled burns, or "let burn" policies, into management plans to improve or maintain moose habitat. The useful life of a burn for moose has been estimated at less than 50 years with moose densities peaking 20-25 years after the burn (LeResche *et al.* 1974). Spencer and Chatelain (1953) estimated that three years elapsed before the 1947 burn on the Kenai Peninsula produced significant amounts of browse. Spencer and Hakala (1964) stated that plant communities from 5 to 20 years post-fire were optimum in terms of moose forage. These results suggest that in some habitats the immediate benefits of fire to moose may be negligible. Furthermore, managers may have to compensate for an initial short-term loss of moose habitat in burning programs. Prompt use of burns by moose has been observed, however. Peek (1974) reported increasing moose populations in the Little Sioux burn in Minnesota the first two winters after the fire. Gasaway and Dubois (1985) found that moose continued to occupy their traditional home range during and after a slow moving, patchy fire in interior Alaska.

Few data are available to provide estimates of browse regrowth and use by moose in Alaska

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less than three years after a burn (Wolff and Zasada 1979). This information is essential to assess the feasibility of fire as a management tool, select specific sites for burning, determine burn size and frequency, estimate short-term fire effects on moose, and to incorporate specific sites into wildlife and fire management plans.

The purpose of this study was to estimate browse regrowth and use by moose two months to two years after a fire in interior Alaska. A second objective was to examine yearly trends in browse nutrient composition following the fire, as well as differences among species.

Study Area

This study was conducted in the 1983 Rosie Creek burn, about 40 km southwest of Fairbanks, Alaska. The fire began on 29 May and was brought under control in 17 days (Juday 1985). About 3,500 ha of upland forest and Tanana River valley bottomland was burned. Most of the burn was on upland sites with east, southeast, south or southwest aspect. Plant communities burned included 130- to 180-year-old (based on tree coring) white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (Mill.) B.S.P.), and paper birch (*Betula papyrifera* Marsh.) forest. Younger (63- to 72-year-old) white and black spruce and quaking aspen (*Populus tremuloides* Michx.) forest were also consumed, as well as some mesic bottomland herbaceous communities.

The fire was hot and fast moving (Juday 1985). A convective fire storm, which generated winds over 160 km/hour, uprooted 16 ha of mature (48 cm diameter breast height) white spruce forest. Although specific areas could be classified as light or heavily burned, the burn pattern was fairly uniform. Islands of unburned vegetation within the fire perimeter were rare. Preliminary results of research associated with this fire were reported in Juday and Dyrness (1985).

Vegetation of the area before the fire was typical for the Tanana River floodplain or Yukon-Tanana uplands. Quaking aspen stands had a closed canopy. The shrub layer was composed of high bushcranberry (*Viburnum edule* (Michx.) Raf.) and prickly rose (*Rosa acicularis* Lindl.). The low shrub layer was dominated by buffaloberry (*Shepherdia canadensis* (L.) Nutt.), twinflower (*Linnaea borealis* L.) and kinikinnick (*Arctostaphylous uva-ursi* (L.) Spreng.). Important herbaceous species were bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.), bedstraw (*Galium boreale* L.), and horsetail (*Equisetum scirpoides* Michx.); leaf litter covered the soil surface. Some white spruce were also present.

Paper birch stands had well-developed, open canopies with scattered white spruce and quaking aspen. The understory was dominated by the tall shrubs; green alder (*Alnus crispa* (Ait.) Pursh.), prickly rose, and high bushcranberry. Important herbaceous plants were bluejoint, horsetail (*E. arvense* L.), and bunchberry (*Cornus canadensis* L.). Litter covered the soil surface.

The mature white spruce forests had open canopies with a few aspen and birch. The tall shrub layer was sparse with green alder, prickly rose, and high bushcranberry. Low shrubs included twinflower and mountain-cranberry (*Vaccinium vitis-idaea* L.). Herbaceous species included horsetail, wintergreen (*Pyrola secunda* L.), and *Geocaulon lividum* (Richards.) Fern. A well-developed moss-lichen mat covered the forest floor. Stair-step moss (*Hylocomium splendens* (Hedw.) B.S.G.) and chink moss (*Pleurozium schreberi* (Brid.) Mitt.) were most abundant. Lichens included *Peltigera* spp. and *Cladonia* spp.

A 70-year-old white spruce forest had a greater density of trees, but they were small in height and diameter. The tall shrub layer was dominated by Bebb willow (*Salix bebbiana* Sarg.).

The bottomland black spruce forest had an open canopy, and trees were small in height and diameter. Tall shrubs present were prickly rose and high bushcranberry with scattered willows (*S. glauca* L., *S. bebbiana,* and *Salix* spp.). The low shrub layer was dominated by Labrador tea (*Ledum groenlandicum* Oeder.), mountain-cranberry, and bog blueberry (*V. uliginosum* L.). Important herbs were bluejoint, horsetail (*E. silvaticum* L.), and *G. lividum.* A thick mat of moss (*Sphagnum* spp., *Hylocomium splendens, Polytrichum* spp., *Pleurozium schreberi*) and lichen (*Peltigera* spp., *Cladonia* spp.) covered the soil surface.

Upland black spruce forests had a more developed, open canopy and trees were taller and larger in diameter. The understory was similar to bottomland stands, except for the addition of

green alder. Plant names follow those given by Hulten (1968), Viereck and Little (1972), and Crum (1976).

The density of moose on the study area was unknown. The Alaska Department of Fish and Game estimated an average of 0.97 moose/km² in Game Management Unit 20B, which encompasses the study area. Moose densities ranged from 3.8-0.2/km² in 20B, depending on locale. Moose density on the study area was considered low because of the area's proximity to Fairbanks and good access for hunters.

Methods

During June 1983, 10 study sites were established at random with respect to moose occurrence on the study area. Study sites were located in stands homogeneous with respect to pre-fire plant community and topography. Sites were chosen primarily for other fire ecology studies, and represented the variability in topography and stand age that occurred in the study area for each of the four major palnt communities burned. Two sites were in 70-year-old aspen forest on primarily south-facing slopes of 33 and 36 percent, respectively. A third site (70-years-old) was in a mixed aspen-white spruce stand on a moderate (18%) south slope, adjacent to the other aspen sites.

Two sites were located in 130- and 136-year-old paper birch forests. The younger site was on a ridge with a 5 percent slope of southwest aspect, while the other was on a steep (30%), southeast-facing hillside.

Three sites in white spruce forest were also studied. Two of these were in 190- and 180-year-old stands. The older stand was within the area of the fire storm. Aspect was south and the slope was 20 percent. The other site was on a southwest-facing slope of 27 percent. The 70-year-old white spruce stand studied was on an 18 percent slope with southwestern exposure.

Two black spruce stands were also sampled. One was on an old river terrace that also burned in 1914; the other was an upland site on a mid-slope bench. Trees at the upland site were about 140 years old and the area was primarily flat with little topographic relief on a 2 percent north-facing slope. Permafrost occurred only at the black spruce sites. Information on herbaceous and woody biomass for the first two summers after the fire was given in Viereck and Foote (1985).

At each site a grid system was established to define plot locations. Twenty points were delineated in a 50 x 40 m grid with points every 10 m. Grid configuration was modified at two sites to 100 x 20 m in order to remain within a uniform stand.

During the summers of 1983-85, browse density was estimated at each site in 20 circular plots. Plot size varied with stand density. In aspen stands, a 4-m² plot was used, but in birch and spruce stands, where browse regrowth was primarily from stump sprouts, we used either 10-m² or 50-m² plots. Browse density was estimated for each species by counting individual stems rooted within a plot.

During mid-May 1984 and 1985, before plant growth began, winter browse use by moose was estimated at each site. Browsed and unbrowsed stems were counted in each plot, providing an estimate of percent use. The basal diameter, height, and diameter at the point of browsing (DPB), if applicable, were also measured for each individual stem. Height was measured to the nearest centimeter with a steel tape, and diameters to the nearest 0.01 mm with a dial caliper.

In 1984, plots were examined in numerical order until 100 stems of each species were sampled. However, a modified sampling scheme was used in May 1985; five plots were chosen at random. The same measurements were made as in 1984, except that only 20 browsed stems per plot were measured for height and diameter. If 100 total stems were not counted or 50 browsed stems were not measured, additional plots were randomly sampled until those criteria were met. The number of twigs per stem was also recorded in 1985 because of extensive branching of some species.

To estimate browse biomass eaten by moose, a sample was collected during May 1985 from unbrowsed stems representative of portions removed by moose. From each site, 10 individuals of each browse species were clipped at diameters within the range of DPB's measured in the stand. Clipped samples were oven-dried at 60°C for 48 hours and weighed to the nearest 0.01 g. From these samples, regression equations were developed to predict browse biomass eaten by moose (y) from DPB (x) (Telfer 1969, Grigal and Moody 1980, Oldemeyer 1983). Exponential equations

[logn y = a(logn x)^b] described browse growth most accurately. Browse biomass eaten by moose was equal to mean biomass eaten per browsed stem multiplied by the density of browsed stems, and the mean number of twigs per stem at each site, for each species. Browse use was also estimated with biomass data. The percent of biomass used was equal to biomass eaten by moose divided by available biomass for each species.

Total browse biomass (standing crop) was sampled at each site in mid-July 1984 and 1985 after the cessation of twig growth. Procedures followed were similar to those used in estimating biomass eaten by moose. First, a browse-density estimate was obtained, then regression equations were developed to predict total browse biomass per individual stem based on stem basal diameter. A mean weight per individual stem was then multiplied by stem density. To develop these regression equations, 10 entire plants of each species were clipped during mid-July 1984-85, the leaves and woody materials separated, oven-dried, and weighed. Total browse biomass estimates include the biomass removed by moose during the previous winter.

Generally, available biomass is defined as the amount of material between maximum snow depth and the maximum reach of moose. Wolff and Zasada (1979) used 0.5 and 3 m, respectively. However, during this study, moose browsed as low s 20 cm and browse regrowth did not exceed 2 m. Furthermore, snow accumulation was not significant enough to effect moose foraging until late winter. Therefore, all biomass was potentially available to moose, and browse use was restricted primarily by characteristics of moose behavior, such as forage preference and maximum bite size. We estimated available biomass by multiplying the mean weight of browse eaten per stem by mean stem density and mean twigs per stem for each site in 1984 and 1985.

Browse samples were collected at seven sites in June 1983 and all 10 sites in May 1984 and 1985 for chemical analyses. Up to 100 twigs per species per site were collected for analysis. Plant samples were ground in a Wiley mill to pass through a 1-mm mesh screen. Samples were analyzed in duplicate by the Forest Soils Laboratory, University of Alaska Fairbanks, for crude protein (N x 6.25), phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K) according to A.O.A.C. (1970) procedures. Minerals (ppm), excluding P, were determined with an atomic absorption spectrophotometer; P was estimated with an auto-analyzer.

During early 1984 and 1985, snow depths were measured at random at representative sites for each plant community. Snow was measured to the nearest centimeter at 3 to 10 locations at each site sampled. Average maximum snow depth per site was estimated for each year.

Because each site selected for study was unique in topography or stand age, no statistical comparisons were made among sites. However, *t*-tests were used to compare mean snow depth between years (1984-85). A one-way ANOVA, followed by Tukey's mean separation procedure, was used to test for differences between years (1984-85) in protein and mineral concentrations. The same tests were also used to examine differences in nutrients among the major browse species using data from 1983-85. Statistical significance was accepted at $P < 0.05$.

Results

Browse regrowth after the fire was primarily quaking aspen, paper birch, and willows (*S. bebbiana, S. glauca,* and *Salix* spp.). These plants were the most important to moose in terms of forage production and use (Table 1). Prickly rose, green alder, high bushcranberry, and American red raspberry (*Rubus idaeus* L.) also came in after the fire but were not eaten by moose.

Browse Density, Biomass, and Use

Aspen regrowth was primarily from root suckers and resulted in dense stands (> 300,000 stems/ha at one site) within two months after the fire. Aspen density was highest in aspen stands followed by birch, white spruce, then black spruce stands. Aspen invaded black spruce sites through seedling establishment. Total biomass of aspen regrowth among sites followed a pattern similar to that of stem density (Table 1).

Paper birch regrowth was exclusively from stump sprouts in 1983. By 1985, birch seedlings were becoming established in some spruce and aspen stands. Maximum density of birch was 10,240 stems/ha at a birch site. White spruce stands had the next highest density of birch followed by black spruce and aspen stands (Table 1).

TABLE 1. Mean (SE) density, biomass, and use estimates of browse regrowth in four plant communities after the Rosie Creek fire in interior Alaska. Sampling occurred in 1983-85.

Pre-fire Plant Community and Species	Stems/ha	%[a] Use	Total Biomass (kg/ha)	Available Biomass (kg/ha)	%[b] Use	Biomass[c] eaten by moose (kg/ha)
Quaking aspen						
Quaking aspen	125,218 (45181)	7 (6)	1,667 (478)	177 (72)	11 (6)	19 (16)
Paper birch	367 (367)	0	1 (1)	1 (1)	0	0
Paper birch						
Quaking aspen	2,289 (2111)	34 (1)	54 (53)	4 (3)	50 (23)	2 (2)
Paper birch	8,886 (1354)	38 (5)	58 (8)	8 (1)	38 (4)	3 (1)
Willow	2 (2)	0	Tr	Tr	0	0
Black spruce						
Quaking aspen	1,199 (189)	0	3 (2)	2 (1)	0	0
Paper birch	404 (17)	0	0 (7)	6 (3)	0	0
Willow	1,557 (1484)	30 (30)	18 (18)	5 (5)	40 (9)	2 (2)
White spruce						
Quaking aspen	3,031 (1634)	1 (1)	61 (59)	9 (7)	2 (2)	Tr
Paper birch	2,280 (2131)	23 (10)	42 (35)	4 (3)	20 (9)	1 (1)
Willow	10,882 (10882)	47 (12)	395 (395)	12 (12)	50 (19)	6 (6)

[a]Based on density estimates.
[b]Based on biomass estimates.
[c]Calculated as mean weight per twig browsed x twigs per stem x stem density.
Note: Tr = less than 0.1.

Willow regrowth was from root crowns immediately after the fire and was highest (10,000 stems/ha) at the 70-year-old white spruce stand (Table 1). The only other site with a significant amount of willow was the younger black spruce stand. In 1985 willow seedlings were established at the upland black spruce site.

Trends in total biomass of browse regrowth among stands and species were similar to patterns in stem density (Table 1). Total biomass of all browse species combined averaged 1,668(470) [$\bar{x}$(SE)] kg/ha at aspen sites, 498(398) kg/ha at white spruce, 111(61) kg/ha at birch, and 25(22) kg/ha at black spruce sites.

Available biomass of aspen averaged 66(40) kg/ha in 1984 and 48(25) kg/ha in 1985. Willows followed a similar trend; 32(18) kg/ha compared to 10(8) kg/ha in 1984 and 1985, respectively. Available biomass of birch was 3(1) kg/ha in 1984 and 10(3) kg/ha in 1985.

Browse use was highest on willows followed by birch, then aspen (Table 1). Trends in browse use among stands were directly related to use patterns among species. Moose foraged in the burn the first winter after the fire. Use of aspen, averaged over all sites with aspen and based on stem counts, was 11(4) percent during winter 1983-84. Use of paper birch averaged 47(8) percent during the first winter. Use of willows averaged 46(12) percent over the two sites with willows in winter 1983-84.

Browse use patterns changed at aspen sites during winter 1984-85. Stands browsed the first winter were not used in 1984-85 and vice versa. Use of birch was more consistent between the two years in that most sites browsed the first winter were browsed the next, and use of willow remained the same [47(11)%] each winter.

Browse use estimates based on biomass figures were similar to those based on stem counts (Table 1). A rank-order correlation (Snedecor and Cochran 1967:193) showed a significant positive relationship ($r_s = 0.89$, $P < 0.01$) between the two methods.

Estimates of biomass removed by moose ranged from a high of 51 kg/ha for aspen to a

low of 0.1 kg/ha for birch and are summarized in Table 1. During the first winter, moose removed 13(13) kg/ha of aspen over all sites, but only 2(1) kg/ha during winter 1984-85. Biomass of birch removed was 1(1) kg/ha in 1983-84 and 3(1) kg/ha the second winter. Willows followed a similar pattern, ranging from 17(12) kg/ha removed to 24(19) kg/ha from one winter to the next.

Snow Depths

During winter 1983-84, maximum snow depth (averaged over all sites measured) was 39(6) cm, but during winter 1984-85, average maximum snow depth was 81(1) cm ($t = 5.85$, $P < 0.0005$).

Browse Composition

Protein and mineral content of browse varied among sites (Table 2). However, no clear trends were apparent in this data.

There were some differences in protein and mineral concentrations in the three browse species between 1984 and 1985 (Table 3). Concentrations of K were greater in 1984 than 1985 for aspen ($F = 4.00$, $P < 0.05$), (birch $F = 7.72$, $P < 0.05$), and willows ($F = 7.45$, $P < 0.05$). Furthermore, protein ($F = 8.76$, $P < 0.01$) and P ($F = 17.17$, $P < 0.01$) levels were greater in 1984 than 1985 in birch samples.

Differences among species in protein and mineral levels were also evident (Table 3). Paper birch samples had greater ($F = 5.26$, $P < 0.01$) levels of crude protein than aspen or willows. Aspen was higher ($F = 7.51$, $P < 0.01$) in K than birch, and both aspen and willows had greater ($F = 9.52$, $P < 0.01$) Ca concentrations than birch.

Discussion

The Rosie Creek fire occurred in early spring while plants were still dormant and root reserves were unused. This allowed for rapid regrowth of the three major browse species within two months after the fire. Browse was well established by the end of the summer, which provided moose with abundant forage that winter.

Pre-fire stand age played a significant role in browse response to fire. The aspen, white spruce, and black spruce stands that had burned in 1914 (70-year-old) produced 10-times as much browse as the older (130- to 180-year-old) birch, white spruce, and black spruce stands combined. This was largely due to the high production of aspen stands. In addition, when contrasting young and old black spruce or white spruce stands, three-times as much browse was produced in the younger stands.

Moss and organic surface layers were burned off at many sites exposing mineral soil which is

TABLE 2. Mean (SE) concentration of protein and four elements in browse species collected from four plant communities in the Rosie Creek burn in interior Alaska. Plants were sampled in June 1983 and May 1984-85.

Pre-fire Plant Community and Species	Crude Protein (%)	Macroelements (ppm)			
		P	Ca	Mg	K
Quaking aspen					
Quaking aspen	3.5 (0.1)	950 (50)	4,833 (416)	1,033 (117)	5,067 (377)
Paper birch					
Paper birch	7.5 (0.6)	1,384 (17)	3,200 (326)	734 (36)	3,450 (150)
Quaking aspen	5.0 (1.8)	733 (133)	4,100 (462)	1,167 (120)	5,167 (684)
Black spruce					
Paper birch	6.6 (1.3)	1,400 (212)	2,750 (300)	775 (25)	4,350 (495)
Willows	3.9 (0.7)	900 (153)	4,767 (696)	767 (176)	3,833 (940)
Quaking aspen	4.5 (0.9)	1,200 (82)	8,400 (903)	1,300 (201)	6,200 (401)
White spruce					
Quaking aspen	4.9 (0.8)	1,400 (231)	6,033 (848)	1,200 (104)	5,800 (737)
Paper birch	4.7 (0.3)	1,067 (260)	3,517 (584)	700 (100)	3,367 (400)
Bebb willow	3.3 (0.4)	900 (58)	6,067 (410)	533 (219)	5,067 (1386)

TABLE 3. Mean (SE) concentration of protein and four elements in twigs of three browse species collected from four plant communities in the Rosie Creek burn. Sampling occurred in June 1983 and May 1984-85.

Species and year	Crude Protein (%)	Macroelements (ppm)			
		P	Ca	K	Mg
Quaking aspen					
1983	7.1 (2.1)	1,700 (182)	6,200 (450)	5,900 (700)	1,300 (100)
1984	4.6 (0.5)	1,100 (71)	6,000 (286)	5,700 (464)	1,200 (71)
1985	3.6 (0.4)	700 (45)	4,000 (409)	4,100 (364)	900 (182)
Paper birch					
1983	8.6 (0.9)	1,700 (150)	3,600 (150)	3,300 (273)	900 (91)
1984	5.8 (0.7)	1,200 (77)	4,400 (400)	3,300 (280)	900 (80)
1985	3.9 (0.5)	800 (100)	2,800 (150)	3,000 (550)	600 (150)
Willows					
1983	4.5 (0.4)	1,000 (71)	3,200 (71)	5,100 (213)	700 (1)
1984	3.8 (0.4)	1,100 (71)	6,800 (1064)	6,100 (142)	1,000 (142)
1985	2.6 (0.1)	700 (71)	3,400 (709)	5,100 (1631)	300 (213)

necessary for seedling establishment (Viereck 1973). By the third growing season after the fire, seedlings of the three major browse species were present at many sites. Seedlings were primarily of the dominant species at each site, but each browse species invaded some sites, most notably black spruce stands. If invading seedlings survive, the poorer sites in terms of browse regrowth may become good foraging habitat for moose.

Browse use by moose in the Rosie Creek burn was scattered and locally concentrated. The large area burned and low pre-fire moose population was responsible for this use pattern. Moose were able to forage away from the most accessible areas of the burn and salvage-logging operations. In addition, moose did not use browse in the area of the firestorm. The large-diameter trees that were uprooted by the firestorm formed a physical barrier excluding moose.

Differences in snowfall between winters also affected use patterns at aspen sites. The above-normal snowfall of the second winter laid down and buried many aspen suckers, especially those on steep slopes. Many birch stems were also buried. In comparison, willow stems which were over 1 m tall were used at the same rate each winter.

We found a significant ($P < 0.05$) positive correlation in estimates of browse use when derived from stem counts or biomass sampling. Regelin (1987) reported similar findings when estimating use of paper birch and suggested that labor intensive biomass sampling be redirected toward counting more twigs and thus increasing sample size, and the precision of use estimates. Our results add further support to this conclusion.

Generally, protein and mineral concentrations in the browse species that we examined were greatest in 1984 and some nutrients declined significantly ($P < 0.05$) in 1985. It appears that most nutrients made available by fire are quickly absorbed by resprouting plants, and that this benefit of fire is relatively short-lived compared to the increase in browse biomass.

Schwartz *et al.* (1987) reported that moose need a minimum dietary crude protein content of 6.8 percent to meet maintenance needs. Paper birch samples in this study exceeded that amount at all but one site. However, aspen and willows were all below 6.8 percent. Contrariwise, K and/or Ca levels were greater in aspen and willows than birch. The minimum requirements of these minerals for moose are unknown. However, these results support the suggestion of Oldemeyer *et al.* (1977) that moose may use a variety of browse species to meet their nutritional needs.

The results of this study and others conducted in interior Alaska provide land managers with information that should be incorporated into burning programs designed to improve moose habitat. Burning should be done in early spring as soon as the area will carry a fire. A hot fire will burn off moss and organic layers providing a good seedbed, yet still allow for sprouting of trees and shrubs. A mosaic of burned and unburned vegetation will allow moose to remain in the immediate area during the burn (Gasaway and

Dubois 1985). A variety of plant communities should be burned to provide immediate and long-term browse regrowth, as well as diversity of browse species (Wolff and Zasada 1979). Aspen and willow provide immediate and abundant browse after a fire. Younger stands that may currently be good moose foraging habitat should be burned because these stands are the most productive and will result in the greatest immediate success of the program.

Acknowledgments

The authors thank P. Adams, E. Deehan, J. Foote, and C. Williams for their assistance in data collection. J. Levison performed the nutrient analysis of browse samples.

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Received 2 January 1989
Accepted for publication 13 October 1989

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Habitat Use and Movement Patterns by Migrating Mule Deer in Southeastern Idaho

Abstract

Relocations of radiocollared mule deer (*Odocoileus hemionus*) captured on two winter ranges in southeastern Idaho indicated that deer associated with the winter ranges occupied summer ranges spread over a >6,000 km² area. Most marked animals summered on public lands in mountainous areas east and southeast of the winter ranges. Autumn migration occurred in October-November. Spring migration occurred in March-May. Most marked deer migrated along definable corridors and used the same corridors in spring and autumn. Migration corridors followed prominent geographic features, and deer selected open vegetation types within corridors. The observed habitat use and movement patterns showed that deer migrating from one of the largest winter concentration areas in southeastern Idaho were not exposed to excessive hunting pressure during migration nor were their migration corridors immediately threatened by human land use. Areas where deer concentrated in migration corridors were identified and these areas should be protected from overgrazing and excessive conversion of native vegetation to crop production.

Introduction

Long distance movements between seasonal ranges are common in mule deer populations in the northern Rocky Mountains (Wallmo and Regelin 1981). Migration allows animals to make optimal use of vegetation with pronounced seasonal changes in quality or availability and to minimize the negative energy balance deer in the Rocky Mountains face during winter (Geist 1981, Wallmo and Regelin 1981, Garrott *et al.* 1987). These benefits are gained at the expense of increased exposure to predation or accidents as animals move between widely separated seasonal ranges.

As the intensity of human land use has increased in the Northwest, so has the potential for animal mortality increased along migration routes. Deer must negotiate highways, intensive agriculture, subdivisions, urban areas, and changes in harvest regulations as they pass through different administrative jurisdictions on their journey from summer to winter ranges. Quantitative information on migration timing and routes is difficult to obtain in the northern Rocky Mountains because of the inclement weather and the restrictions to observer ground mobility enforced by the snow and/or mud common during migration periods.

Information on migration patterns is sparse for mule deer using winter concentration areas in southeastern Idaho. The Idaho Department of Fish and Game initiated a radiotelemetry study of mule deer on two winter ranges in southeastern Idaho in 1983 to determine movement patterns, habitat use, and vulnerability of these deer to impacts associated with human land uses. This paper addresses three questions relative to movement, habitat use, and vulnerability during migration:

1) What is the timing and spatial pattern of migration?
2) What vegetation and which physiographic features are important to deer during migration?
3) Are migrating deer threatened by hunting and human land use during migration?

Study Area

The Willow Creek Winter Range (Figure 1), a 155-km² canyon complex 20 km east of Idaho Falls, provides a wintering area for a minimum of 3,000 mule deer (Thomas 1987). Elevation ranges from 1550-1950 m, annual precipitation averages 43 cm, and average annual temperature is 5°C. The shrub steppe vegetation of the Willow Creek area is dominated by sage (*Artemesia tridentata* and *tripartita*)—wheatgrass (Agropyron)/needlegrass (*Stipa*) habitat types with scattered juniper (*Juniperus osteosperma* and *scopulorum*) and aspen (*Populus tremuloides*) stands in canyon breaks and willow (*Salix* spp.) thickets along streams. Three-quarters of the plateau area above the canyon complex had

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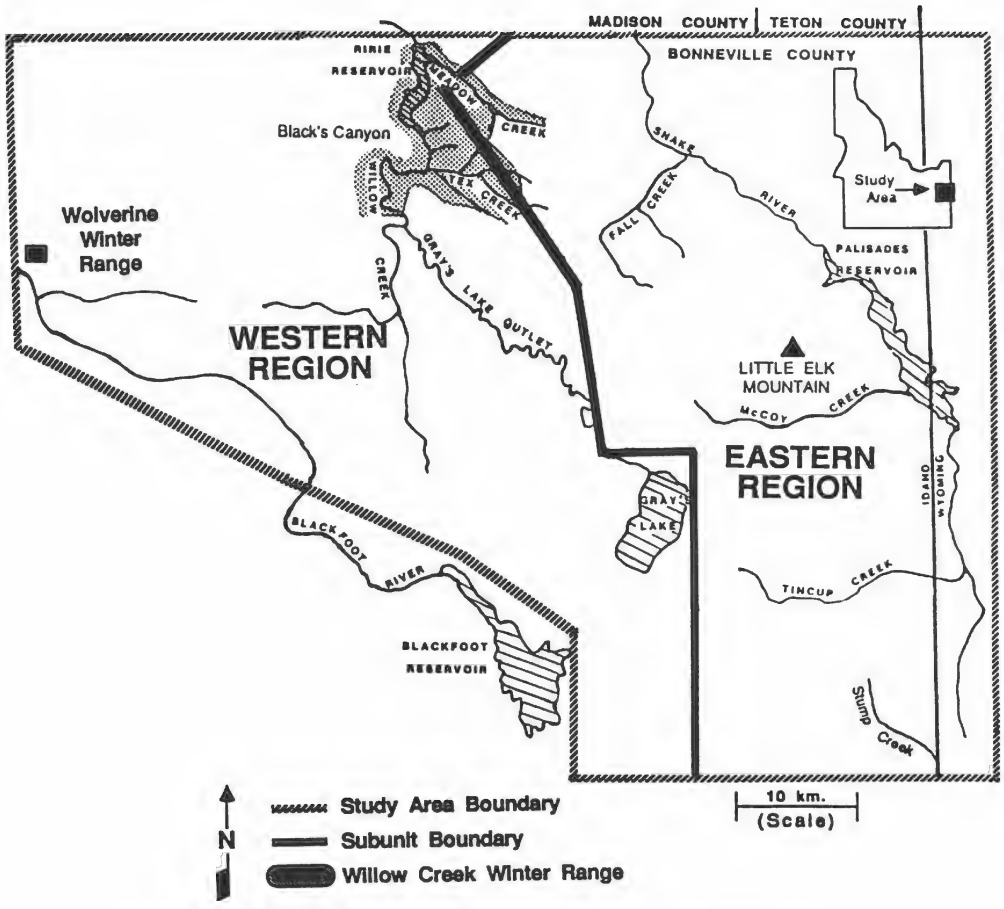

Figure 1. Map of the area occupied by mule deer associated with the Willow Creek and Wolverine winter ranges.

been converted to dryland wheat production at the time of this study. Movement information was supplemented by deer associated with wintering areas 30 km west of Willow Creek along Wolverine Creek. The 10-km² subunit in which deer were captured is similar in vegetation and land use to the Willow Creek area.

Land west of the winter ranges is similar in topography, vegetation, and land use to the shrub steppe surrounding the winter ranges. Land east of the winter ranges is dominated by foothills, mountains, and the Snake River Valley. Elevations range from 1,550-3,000 m. Vegetation varies from shrub steppe on dry (usually lower elevation) sites to aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*) forests on wet (usually higher elevation) sites.

Methods

Eighty-eight mule deer were captured on the Willow Creek Winter Range and 66 on the Wolverine Winter Range (Figure 1) during 1983-86 using dropnets, helicopters and collapsible drive-nets, or Clover traps (Clover 1954, Ramsey 1968, Beasom *et al.* 1980). Thirty animals (26 from Willow Creek and 4 from Wolverine) were fitted with radio-transmitters (Telonics, Mesa, AZ), 51 with individually coded urethane collars (Ritchey Manufacturing, Brighton, CO), and 15 with colored plastic eartags. All animals were marked with numbered metal eartags.

Radiocollared deer were relocated at 3-14 day intervals during January 1984-November 1986 from a fixed wing aircraft. Sights of collared, eartagged, and radiocollared animals by hunters and resources agency personnel were used to supplement radio relocations. Aerial relocations were recorded to 0.01 minutes of latitude and longitude using LORAN C navigational receivers interfaced to an onboard computer (F. Reed, Western Air Research, Driggs, ID). Small scale corrections were made when the pilot's description (notes on terrain form, vegetation growth form, and aspect entered in the onboard computer at the time the LORAN location was entered) and/or 35 mm photographs taken at locations did not agree with LORAN locations. Coordinates of all locations were plotted on 7.5-minute USGS topographical maps.

Seasonal home range boundaries were delineated using the minimum polygon method (Mohr 1947, Lonner and Burkhalter 1986). Migration routes were plotted using relocations during autumn and spring migration periods. Migration periods for individual animals were defined as beginning with the first location more than 3 km outside a seasonal homr range without a return movement to the home range and ending with the first relocation on the new seasonal home range. Distances between seasonal ranges were calculated based on distances between summer and winter geographical activity centers (GAC = mean x and y coordinates obtained from all locations within a seasonal home range).

Availability of ground cover types (closed conifer, open conifer, closed aspen, open aspen, open grass/shrubland, agriculture, riparian, other (bare ground, rock, road, buildings, etc.)) in areas used by migrating deer was determined from 46 35-mm transparencies taken at intervals of 2.5 minutes of longitude and latitude from an altitude of 4,930 m a.s.l. These photographs provided a coverage of 95 km² or 18 percent of the 527 km² area associated with the two major migration corridors we identified. The proportion of each cover type on each slide was determined by projecting slides onto a sheet of white cardboard marked with 80 randomly distributed dots. Summed results of counts on all slides were assumed to be representative of the proportions of cover types available. Availability of aspect classes within migration corridors was determined from 80 randomly distributed points within 19 circles, each covering 4 km² on 7.5-minute topographic maps.

Ground cover characteristics of areas used by deer were described, based on the projection of 35-mm transparencies taken at elevations of 100-500 m above ground (coverage of 0.2-3.8 ha per photograph) onto a cardboard sheet with 80 randomly distributed dots. Aspect class and position on slope at deer locations were determined from 7.5-minute topographic maps.

Selection for ground cover type and aspect was determined using a method described by Marcum and Loftsgaarden (1980). Since both habitat availability and deer habitat use were calculated based on clumped subsamples taken at different scales (2 ha per deer location versus 200 ha per habitat location), the null hypothesis tested was: there is no difference between the proportionate distribution of vegetation cover types within a sample of small areas immediately surrounding a deer and the proportionate distribution of cover types sampled in an area roughly half the size of the average seasonal home range of a deer (Thomas 1987) at a series of points selected without regard to deer use. This approach was adopted to minimize biases associated with small scale movements that deer might have made in response to disturbance by the airplane (Jensen 1988) and errors associated with locations in which deer could not be seen. Mean elevation and slope at deer locations were tested against mean values for the study area using Student's t-tests (Steel and Torrie 1982).

Results

Movement patterns

With one exception, a yearling male, all deer followed for more than one year did not shift summer or winter home ranges between years. Radiocollared animals followed similar routes between seasonal ranges in spring and autumn and in different years.

We were unable to identify common migration routes for five of the seven radiocollared animals that summered near or west of winter ranges. Two radiocollared animals that summered near winter ranges and 23 that moved more than 30 km eastward from winter ranges traveled in broad corridors following prominent topographical features (ridges, canyons) oriented toward summer ranges (Figure 2). Corridors

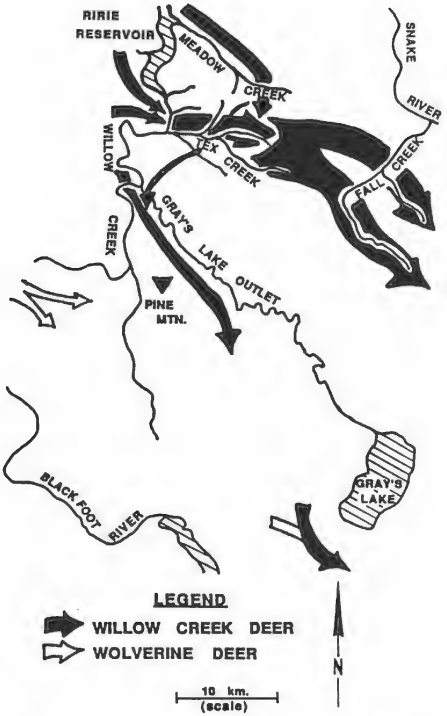

Figure 2. Spring movement patterns observed for mule deer using the Tex Creek-Fall Creek and Gray's Lake Outlet migration corridors.

became increasingly indistinct as distance from the winter range increased. Twenty-four of the 25 radiocollared deer that used defined corridors moved towards summer range through the corridor closest to their winter range. Individuals with adjacent winter home ranges tended to use the same corridors (10 of 14 adjacent pairs). During 1984-86, 112 radio relocations (83 in spring, 29 in autumn) and 12 sightings of neckbanded deer were obtained along definable migration corridors.

Distance between summer and winter GAC's varied from 11 to 115 km for the 29 radiocollared animals that did not shift ranges between years (mean = 54 km, SD = 23). We were unable to identify significant differences in distances between summer and winter GAC's for males (n = 7, mean = 46 km, SD = 34) and females (n = 22, mean = 56 km, SD = 19) (t = 0.66, P > 0.50).

Movement from winter to summer range was characteristically composed of rapid movement of 5-20 km with breaks of 1-10 days between movements. Deer apparently had favored areas, transitional ranges, in which they remained between movements. These areas were used in spring and autumn migrations. We identified four probable transitional ranges in the Tex Creek-Fall Creek migration corridor and one in the Gray's Lake Outlet corridor. These five areas accounted for 71 percent of the 83 spring locations of deer within migration corridors but comprised less than 20 percent of the area traversed during migration. Deer remained on transition areas as late as 8 December during autumn migration.

Individuals varied widely in timing and length of time spent in migration (Figure 3). Mean dates of initiation of spring migration during 1984-86 were 22 May (SD = 9 days), 22 April (SD = 12 days), and 29 March (SD = 15 days), respectively. Time spent in spring migration by individuals averaged 21 days (SD = 9) in 1984, 26 days (SD = 14) in 1985, and 51 days (SD = 24) in 1986. We were unable to detect significant differences in dates of departure between deer that moved more than 60 km between winter and summer range (n = 22) and deer that moved less than 40 km (n = 7 , t = 0.72, P = 0.50).

Mean dates of initiation of autumn migration were 18 November (SD = 20 days) and 11 November (SD = 20 days) for 1984 and 1985, respectively. By 27 December 1984 and 26 November 1985, all deer had begun to move towards winter range. Mean dates of arrival on winter range for 1984 and 1985 were 27 December (SD = 20 days) and 5 December (SD = 15 days), respectively. Deer moving more than 60 km between seasonal ranges (n = 11) apparently did not vacate summer ranges earlier than deer whose seasonal ranges were separated by less than 40 km (n = 7, t = 0.50, P > 0.50).

Habitat Use During Migration

Habitat use during migration was similar during spring and autumn; therefore, habitat use data for the two seasons were combined. Of 112 relocations within definable migration corridors, only 4 percent were on ridge tops or stream bottoms. The remainder were nearly evenly divided between the upper third (31%), middle third (29%), and the lower third (35%) of slopes.

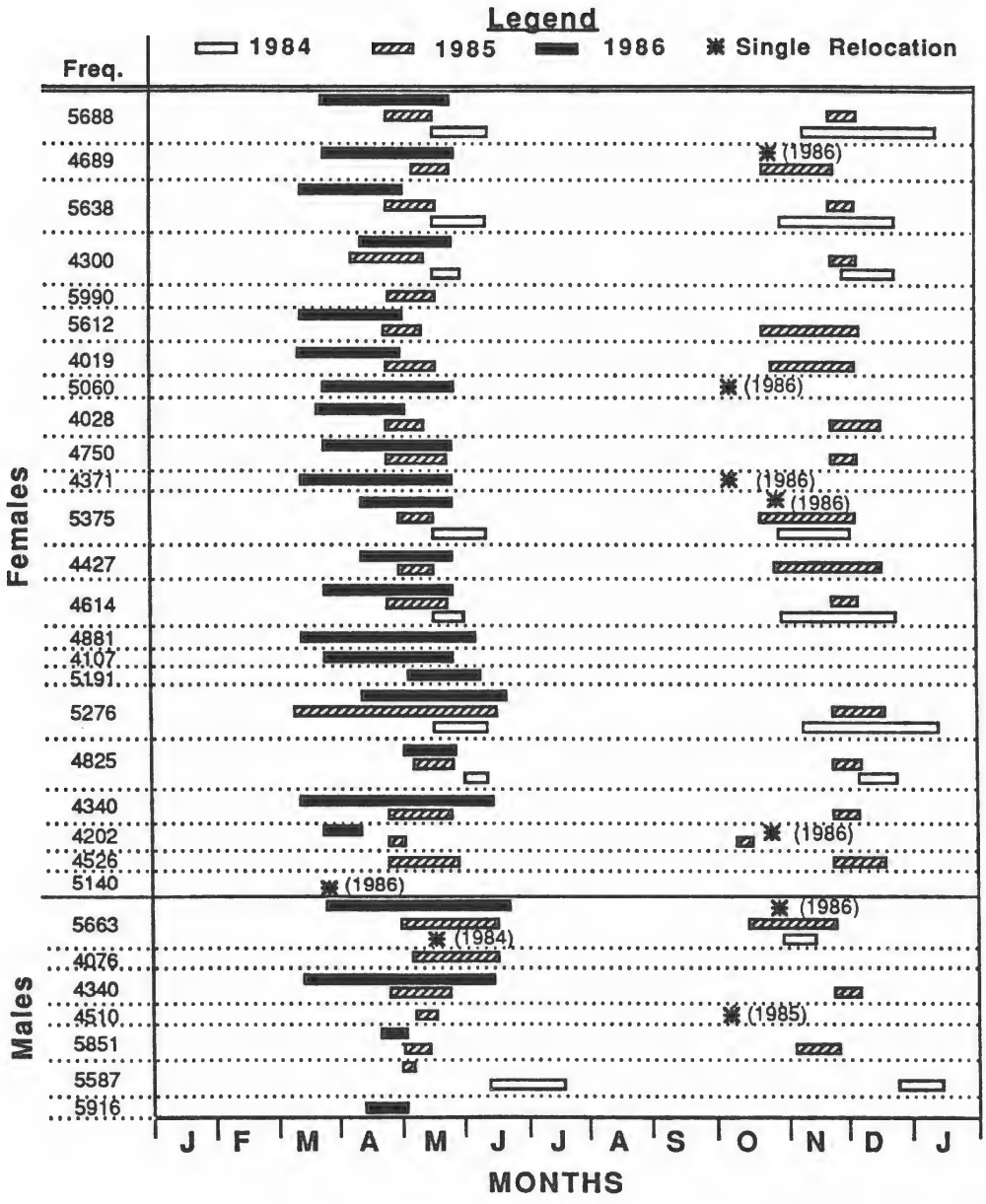

Figure 3. Chronology of spring and autumn migration for 30 radiocollared mule deer marked on the Willow Creek (n = 26) and Wolverine Creek (n = 4) winter ranges, 1984-86. Identification numbers (I.D. #) within sex classes are arranged by distance between winter and summer ranges with animals moving the greatest distances between ranges listed first.

TABLE 1. The distribution of 89 deer locations in the Tex-Fall Creek and 22 locations in the Gray's Lake Outlet migration corridors (% USE) in southeastern Idaho among aspect classes compared with availability of aspects (% AVAIL). Availability was determined from 80 points at each of 19 (13 in the Tex-Fall Creek and 6 in Gray's Lake Outlet corridors) randomly selected locations on topographic maps covering 76 km² within corridors.

	Tex-Fall Creek		Gray's Lake	
Aspect class	% USE	% AVAIL	% USE	% AVAIL
North	9	6	0	9
Northeast	16	23	4	18
East	2	7	46	2
Southeast	9	15	0	3
South	36 *	6	14	7
Southwest	17	10	18	7
West	7	16	0	18
Northwest	3	10	4	8
< 3% slope—riparian and flats	1	6	0	23
< 3% slope—ridgetop	0	1	14	6

* USE differs significantly from AVAIL ($P < 0.05$, Bonferroni simultaneous comparisons). Gray's Lake locations were not tested.

Deer in the Tex-Fall Creek Corridor were located on south aspects in greater than expected frequencies (Table 1). The sample size was too small for statistical analysis by aspect for the Gray's Lake Outlet Corridor, but 10 of 22 locations were on east aspects.

Forty-one usable photographs of deer locations (including 3,279 points at which vegetation cover could be identified) were available for analysis of cover type preferences in the Tex-Fall Creek corridor and 13 (1,031 usable points) in the Gray's Lake Corridor. Areas immediately surrounding radiocollared deer located in the Tex-Fall Creek corridor had higher proportions of open native cover types and lower proportions of closed conifer forests, riparian thickets, and agricultural lands than the high elevation photographs (Table 2). Deer in the Gray's Lake corridor used closed canopy forests and agricultural areas more and open shrub/grassland less than proportionate availability would suggest.

Human Impacts on Migrating Deer

Twenty-six of 29 deer followed during the general hunting season were on their summer home ranges at the opening of the season. In six cases (one male and three females during a single year and one female during two years), deer effectively shortened the time they were vulnerable to harvest by migrating from a hunting unit with a 26-day season to a unit with a 10-day season. In all other instances, deer migrating during hunting season either remained in the hunting unit in which they summered or moved into a unit with a similar season length.

At the time of this study, more than 90 percent of identified migration corridors, 70 percent of lands within 5 km of winter range, and 20 percent of the areas west of winter range used by marked migrating deer (Figure 1) were controlled by state or federal land management agencies. Private lands and human settlements were concentrated in areas west of winter range and along the Snake River and its major tributaries. Approximately 50 percent of land through which deer migrated near winter ranges and west of winter range was used to produce wheat and hay on unirrigated lands. Sheep and cattle were grazed throughout the migration area, with summer grazing dominant on Forest Service lands south and east of the winter ranges and winter or yearlong grazing on low elevation private lands east and west of the winter ranges. Logging and mining were carried out on a small scale within the study area, but no active operations were located in migration corridors.

TABLE 2. Cover type percentages in 41 transparencies taken at mule deer locations (% USE) in the Tex-Fall Creek migration corridor and 13 in the Gray's Lake Outlet migration corridor in southeastern Idaho compared with percentages of cover types in 31 (Tex-Fall Creek) and 15 (Gray's Lake Outlet) transparencies covering 18% of the 527 km² area surrounding the migration corridors (% AVAIL). Percentages are based on the cover types recorded at 80 points per transparency.

Cover type	Tex-Fall Creek			Gray's Lake		
	% USE		% AVAIL	% USE		% AVAIL
Closed canopy conifer	10	*	22	1	*	3
Open canopy conifer	9		8	0		tr[a]
Closed canopy aspen	9		10	8	*	18
Open canopy aspen	3	*	1	0		tr
Open shrub/grass	69	*	52	91	*	66
Riparian	tr	*	1	1		2
Agricultural	0	*	6	0	*	11
Other[b]	1	*	2	tr		1

* USE differs from AVAIL ($P < 0.05$, Bonferroni simultaneous confidence intervals). Cover types with less than 1% availability were not tested.
[a]trace = less than 1%.
[b]Includes bare rock, roads, houses, lakes.

Discussion

The distances moved between seasonal ranges by mule deer in our study area (15-115 km) were characteristic of herds associated with interior mountain-plains complexes in which snowfall limits its access to forage at higher elevations (Leopold *et al.* 1951, Robinette 1966, Mackie *et al.* 1982, Ihsle Pac *et al.* 1988). Migration patterns (direction, initiation, duration, and termination) varied among individual animals and between the years of our study, but most animals moved to mountain or foothill summer ranges through restricted migration corridors. The pattern we observed could be interpreted as avoidance of deep snows (Richens 1967, Gilbert *et al.* 1970, Wallmo and Regelin 1981), population optimization of year-round forage quality (Garrott *et al.* 1987), or a series of individual animals responding to changes in conditions on their seasonal ranges modified by tradition, local weather/microclimatic patterns, disturbance, and knowledge of alternate sites to which they could move (Hamlin 1978, Mackie *et al.* 1982, Ihsle Pac *et al.* 1988).

Migration corridors were associated with prominent geographical features, and were pronounced only where terrain channelized deer movement, tending to become less distinct as distance from winter range increased. The extent to which deer used transitional ranges within migration corridors varied among years. Radiocollared deer apparently did not stop at some transitional ranges when migration coincided with severe autumn weather in 1984 but lingered for 2-4 weeks under the mild weather conditions during the 1985 autumn migration.

The extent of transition range use in spring depended on how early the deer left their winter range. During the three years of this study, deer left winter range latest in 1984, the most severe of the three winters, and earliest in 1986, the mildest of the three winters (Thomas 1987). Use of transition range on Tex Creek was lowest in 1984, moderate in 1985, and heaviest in 1986 (Thomas 1987). This pattern corresponds more closely with that described by Mackie *et al.* (1978) and Ihsle Pac *et al.* (1988) for mule deer in the eastern Rocky Mountains of Montana than with that described by Garrott *et al.* (1987) for the western slope of the Rockies in Colorado.

While in migration corridors, deer apparently selected open, nonagricultural cover types. Preferred aspects supported open vegetation. Position on slopes did not appear to be important since sightings were distributed approximately in proportion to availability of slope classes.

Areas used by migrating deer contained no large cities, and human land use was largely

restricted to agriculture. Deer moving to summer ranges near or west of the winter ranges were evidently not concentrated into narrow corridors during migration. Migration corridors to the east of winter ranges were on public land and accessed only by secondary roads which were generally closed by snow or mud during migration periods.

Hunting was timed so that the general deer season occurred when most deer were on summer range thereby reducing the vulnerability of migrating deer to harvest. The high frequency of sightings on open sidehills during autumn migration may have been partially due to the minimal amount of hunting disturbance in the study area during the migration period. Nyberg (1980) determined that closed canopy cover types were important when migration took place during the hunting season. Bertram and Rempel (1977) suggested that hiding cover was important on transition ranges largely because of hunting activity.

Transition areas along migration corridors provide the last opportunity for deer to gain or maintain weight during autumn and one of the earliest opportunities to regain weight in spring (Wallmo and Regelin 1981, Garrott *et al.* 1987). Agricultural practices along migration routes could negatively impact migrating deer through overgrazing by domestic livestock and, possibly, through the conversion of native vegetation to croplands. Although our analysis indicated that deer were infrequently located in closed forest cover types, aspen patches in predominantly agricultural lands were used during migration, and loss of these patches could deprive deer of cover and/or nutritious forage during migration periods.

Overall, mule deer using the Willow Creek and Wolverine winter ranges do not appear to be threatened by current land uses. Deterioration of habitat used in migration could be minimized by conventional agricultural conservation practices. Land owners (public and private) should be encouraged to protect patches of woody vegetation that are used as diurnal resting sites by migrating deer, to avoid over-grazing pastures, and to maintain a mosaic of crop and grazing lands in areas where crops are grown.

Acknowledgments

We thank R. Mackie, C. Brown, T. Trent, S. Haynes, and J. Connelly for helpful suggestions throughout the study and the many Idaho Department of Fish and Game personnel who provided field assistance. This study was supported by Federal Aid in Wildlife Restoration Project W160-R-13 to the Idaho Department of Fish and Game.

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Received 19 December 1988
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W-Waves and Plant Spacings

Abstract

W-waves have characteristic frequencies in plants. To see if branch patterns might correlate with these frequencies branch, twig, stem, and leaf spacings were analyzed in a number of plants. The distributions of frequencies (Hz) associated with spacings were found to correlate closely with a spectrum analysis of actual frequencies emitted by plants. The distributions appear to be frequency spectra of plant utilized W-waves.

Introduction

Earlier I reported the discovery of W-waves in plants (Wagner 1988a,b; 1989). Evidence for the existence of W-waves consisted of measured electrical patterns, recorded oscillations, excitation behavior, and reflection phenomena. Measured electrical patterns appeared to indicate that standing waves are always present in plants and may play a part in their physiology. Recorded oscillations are another feature that demonstrated the presence of waves. Evidence indicated that the observed waves were not electromagnetic (Wagner 1988b; 1989) but as they interacted weakly with charge it was possible to observe some of their effects with ordinary electrical measurement equipment. I disturbed the apparent standing wave pattern in a tree at different locations and detected oscillatory behavior coming from two probes in the tree; a typical response upon disturbing any standing wave pattern. The velocity of the waves in the tree was found to be 90 ± 6 cm/sec using pulse reflection (Wagner 1988b). All the evidence pointed to the existence of waves in plants.

The presence of standing waves in plants led to the idea that nodes (or antinodes) may be likely places for the growth of branches or other plant structures. To test this hypothesis several thousand branch and other spacings on plants were measured to see if the frequency distributions of plant growth spacings would demonstrate discrete groups.

Observation of such discrete spacings would suggest that the growth spacings are related to the standing waves already observed in plants. As such discrete groupings of spacings were found I attempted to correlate the frequencies from a low frequency spectrum analyzer connected to probes in plants with the frequencies (Hz) calculated from observed plant growth spacings.

Methods and Materials

Measurement of Spacings

Details of the methodology of electrical signal measurements on trees and other plants were described earlier (Wagner 1988a,b; 1989). The plants used in this study grew at an altitude near 460 m. Measurements of plant growth spacings (i.e. distances between branches, twigs, stems, or leaves) were taken with a rule calibrated in millimeters and estimated to the nearest 0.1 mm. It is difficult to measure the spacings between branches, twigs, and leaves on branches accurately without good reference points. A few plants, such as big leaf maple (*Acer macrophylla*) with its bands at branch locations, syringa (*Philadelphus* sp.) or sweet corn (*Zea mays saccarata*), have distinct features which do provide good reference points. For consistency, appropriate reference points were chosen in every case. Spacings between needles on conifers were omitted from these measurements because the spacings are so small. While an attempt was made to take a representative random sample of spacings so that a distribution would be typical of the spacings from a particular species of plant, the spacings of branches on tree trunks were ignored because there were relatively few branches per tree.

The data recorded were spacings between: (1) twigs and small branches on one young (approx. 5 m) white fir (*Abies concolor*); (2) lower branches of three (approx. 30 m) white fir trees; (3) leaves and stems on several prickly lettuce (*Lactuca serriola*) plants; (4) twigs, mostly from lower branches, on two young Douglas-fir trees (*Pseudotsuga menziesii*) (9 m) growing in the open

(emphasizing new but completed growth); (5) twigs on another young Douglas-fir (8 m) growing in semishade; (6) lower branches of 5 approximately 15 m ponderosa pines (*Pinus ponderosa*) growing in a clump with other trees; (7) leaves and branches on one bigleaf maple, cut down for easy access; (8) leaves and branches on one small (approx. 4 m) Oregon ash (*Fraxinus latifolia*); (9) leaves and branches on one syringa shrub; (10) joints on many stalks of sweet corn; (11) leaves and branches on some lower branches of two delicious apple trees (*Pyrus Malus* sp.); and (12) leaves and branches from four different Concord grape (*Vitus labrusca*) vines. No attempt was made to obtain all the spacings from any particular tree or other plant except in the case of prickly lettuce.

The plant growth spacings were analyzed to see if they clustered into discrete groupings by taking the frequency distributions of the measured spacings using 1 mm intervals. Spacing mostly appeared to be discrete (Figure 1). Each spacing in the twelve sets of data above was then converted to a frequency in Hz by dividing a W-wave speed of 96 cm/sec by twice the spacing (see data analysis), (96 cm/sec was within the previously measured wave speed of 90 ± 6 cm/sec (Wagner 1988a,b)). The number of spacings in each 0.1 Hz interval (bin) was plotted against frequency in Hz for each set of data to make the 12 graphs of Figures 2-5. By converting spacings to frequency (Hz) and taking the distribution I could compare frequencies derived from growth spacings directly with frequencies found from spectrum analysis. Any correlation between these frequencies would tend to indicate the W-waves with their wave patterns were involved in setting plant growth spacings. I did not attempt to verify if an existing branch spacing pattern correlated with the *in situ* standing wave pattern in a particular plant as I assumed that the standing wave pattern slowly changes as the plant grows (see Wagner 1988b).

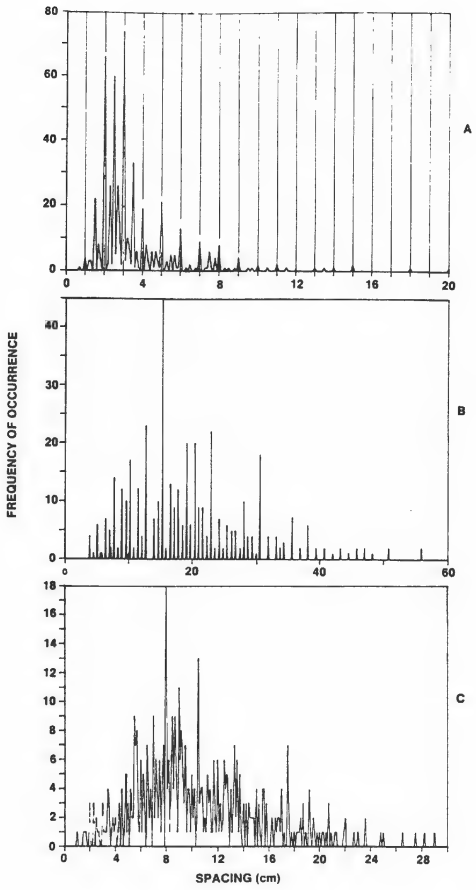

Figure 1. Spacing distributions of (A) 536 branch and leaf spacings from the lower branches of two delicious apple trees, (B) 429 spacings from the lower branches of five ponderosa pine trees (approx. 15 m high), and (C) 502 leaf and branch spacings from Concord grape vines. The interval used in taking the distributions was 0.1 cm.

Measurement of W-wave Frequencies

Direct measurements of the frequency spectrum of electrical signals (Figures 6 and 7) were recorded on a frequency spectrum analyzer (Schlumberger 1201) by placing probes in the plants (Wagner 1988a,b; 1989). Concern for possible 60 Hz interference led to testing the analyzer far away from 60 Hz sources but the same apparent W-wave peaks (harmonics) usually appeared when a 48.8 Hz supply was used. Care was taken to assure that any peak considered as a W-wave peak from the spectrum analyzer was found only in association with plants. Peaks such as 60 Hz harmonics from ac power are common (60 Hz also appears to be a common W-wave frequency) and numerous electronic devices radiate other spurious signals so spectra were taken approximately 1500 times to validate the various

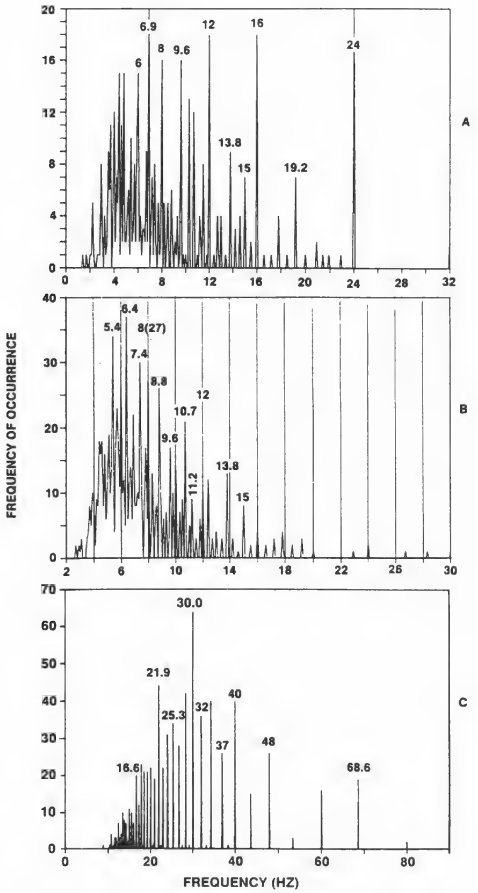

Figure 2. Frequency of occurrence of spacings (converted to frequency in Hz by using f = 48/s where f is the frequency and s is the spacing. See the text) versus frequency (Hz) of branch, twig, stem, and leaf spacings for (A) 489 spacings on a young white fir (5 m), (B) 863 spacings on the lower branches of three 30 m white fir*, and (C) 720 spacings on prickly lettuce. The bin (intervals used in obtaining the distributions) in these frequency distributions is 0.1 Hz. The frequencies above peaks in Figures 2-5 were taken from the Lotus 1,2,3 worksheets used for data analysis.

*Number in parenthesis after a frequency refers to the number of spacings for that peak.

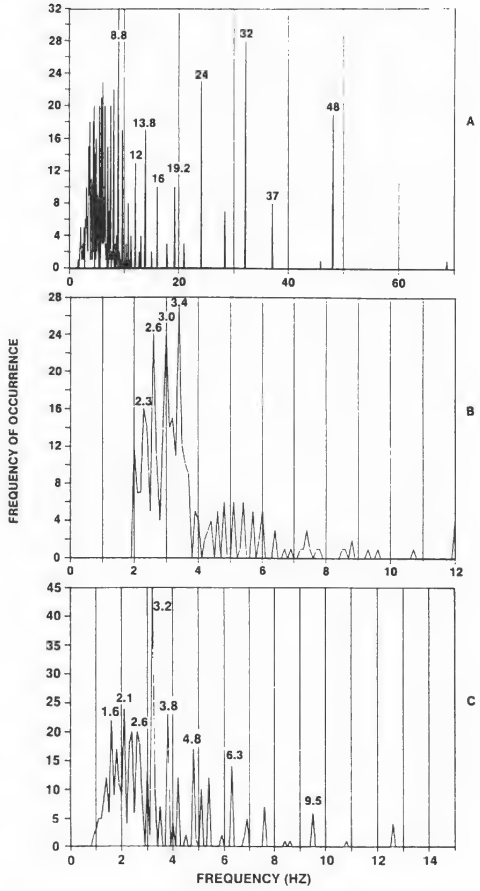

Figure 3. Frequency of occurrence of spacings versus frequency (Hz) for (A) 633 spacings from two Douglas-fir (9 m) growing in the open, (B) 314 spacings from a young (8 m) Douglas fir growing in semishade, and (C) 429 spacings from the lower branches of five approximately 15 m ponderosa pine growing in a clump with several other trees.

apparent W-wave frequencies. Common mode cancellation and coaxial cable with appropriate grounding was used to minimize undesirable signals. No attempt was made to compare amplitudes of the same frequency peak in different plants on the spectrum analyzer. The spectrum analyzer data were taken from 1 July to 8 October 1988.

The spectra were also confirmed, checked, and analyzed in the following ways:

(1) A battery operated instrumentation amplifier in a metal box (a 90 cm aluminum cube) was connected to a potted plant in the same metal box with appropriate probes. A pair of coaxial cables took the signal to the differentially

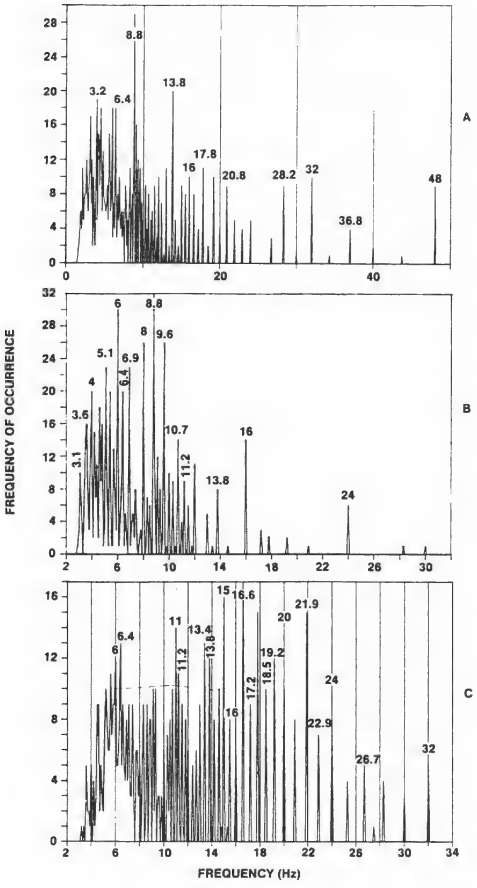

Figure 4. Frequency of occurrence versus frequency (Hz) for (A) 865 branch and leaf spacings from a big leaf maple (approx. 10 m), (B) 622 branch and leaf spacings from a small (4 m) Oregon ash, and (C) 642 branch and leaf spacings from a syringa (shrub).

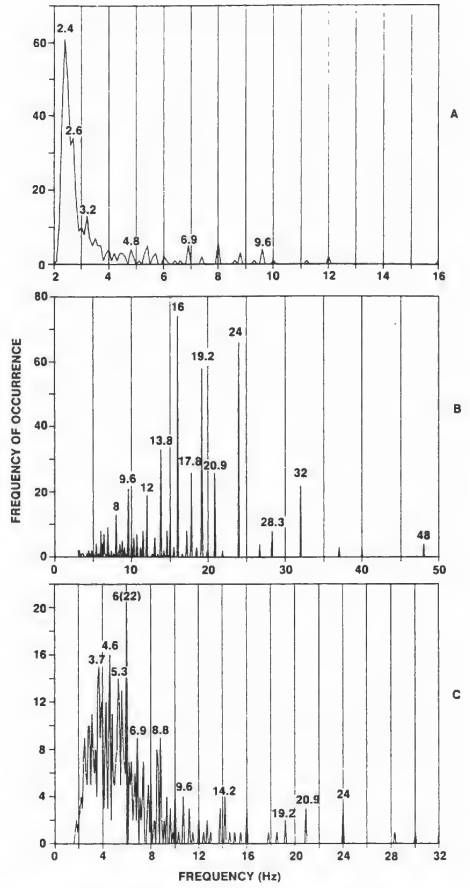

Figure 5. Frequency of occurrence versus frequency (Hz) for (A) 392 joint spacings on sweet corn, (B) 536 branch and leaf spacings from the lower branches of two delicious apple trees, and (C) 502 leaf and branch spacings from Concord grape vines.

connected spectrum analyzer outside the metal box (Figure 8). The amplifier increased the signal amplitude feeding into the spectrum analyzer to the millivolt range with the typical peaks (usually harmonics of 0.16 Hz with certain harmonics that usually are of higher amplitude) I have associated with plants still appearing, but at much higher amplitudes. This confirmed that the observed frequencies were coming from the plant and not the spectrum analyzer. All appropriate measures were taken for common mode cancellation of unwanted signals.

(2) The apparent plant frequencies were also confirmed on a Schlumberger 1220 low frequency spectrum analyzer; a considerably different analyzer which is more sensitive and better designed to reduce spurious responses than the 1201.

(3) Probes in a control dead dry log did not give plant spectra, but they were observed, however, from salt solution filled logs.

(4) Almost all observed peaks appeared to represent harmonics or subharmonics and this fact was used to check peak validity. If the

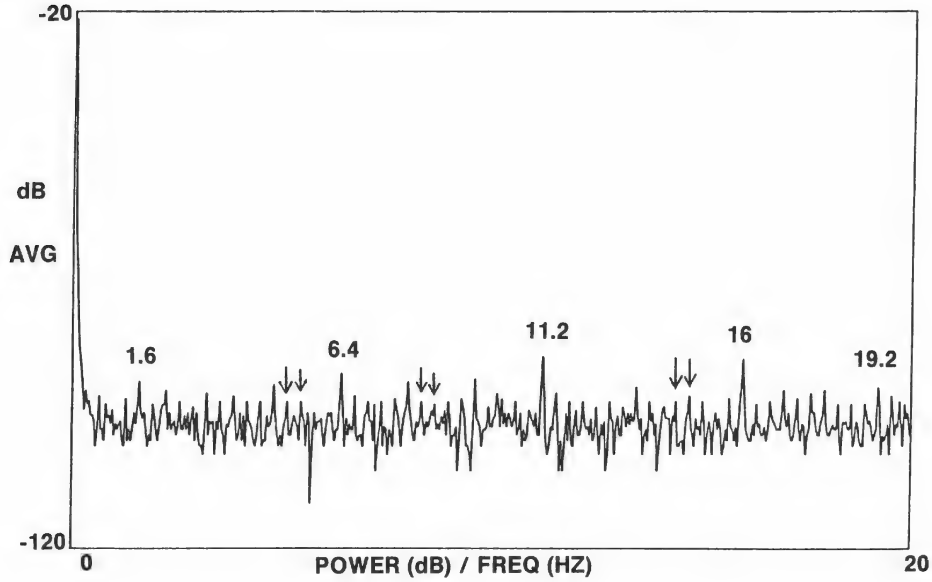

Figure 6. Spectrum (0-20 Hz) from contacts spaced about 3 cm on a willow (*Salix* sp). Notice the peaks spaced at 0.32 Hz and the 1.6 Hz harmonic peaks which often have greater amplitude than the ordinary 0.32 Hz spaced peaks. This spectrum was chosen as rather typical of spectra from plants. Several of the 1.6 Hz harmonic peaks have been marked to indicate the frequency of the peak. This is essentially the same as the spectrum of Figure 7 except that only a detailed portion of the spectrum (baseband 20 Hz) is shown allowing the structure between the 1.6 Hz spaced peaks to be seen. The arrows indicate 0.32 Hz spaced peaks. The scales are linear.

spectrum baseband was set at 30000 Hz peaks were usually observed spaced at 800 Hz (not shown) with the last one at 29600 Hz due to the resolution characteristics of the spectrum analyzer and the nature of the spectrum. If the baseband was set at 2000 Hz the observed peaks were usually spaced at 80 Hz with the 10th peak representing the first 800 Hz peak observed on the analyzer with a 30000 Hz baseband. If the baseband was set at 500 Hz the observed peaks were often spaced at 16 Hz intervals with the fifth peak at 80 Hz or, if the baseband was 100 Hz, the observed apparent plant frequencies were on 1.6 Hz intervals (Figure 7). If the baseband was set at 20 Hz the commonly observed interval was 0.32 Hz, with larger peaks at 1.6 Hz intervals (Figure 6). For basebands of 1 Hz peaks were found at 0.16, 0.08, 0.04, and 0.02 Hz. Characteristically certain harmonics often appear to be larger than others, for example, the 7th and 10th harmonics of 1.6 Hz (11.2 and 16 Hz) using a 20 Hz baseband (note also the larger peaks of Figure 7). There appears to be a regular repeating characteristic pattern in the relative amplitude of harmonics but it has not yet been completely determined. The above harmonics seem to appear only when probes in plants or salt solution filled wood samples are used or from certain other types of sensors in the vicinity of plants (Wagner 1989).

(5) Another technique which appears to confirm the presence of W-wave frequencies involves running a small ac electric current through a plant using one probe near the top and the other near the bottom of the plant. Connecting the spectrum analyzer to two probes in the plant set between the current supply probes indicates that the small ac current frequency beats with W-wave frequencies (Wagner 1989). When the spectrum analyzer reveals a peak at an ac source frequency S, other peaks are also often seen symmetrically placed about this peak. These other peaks

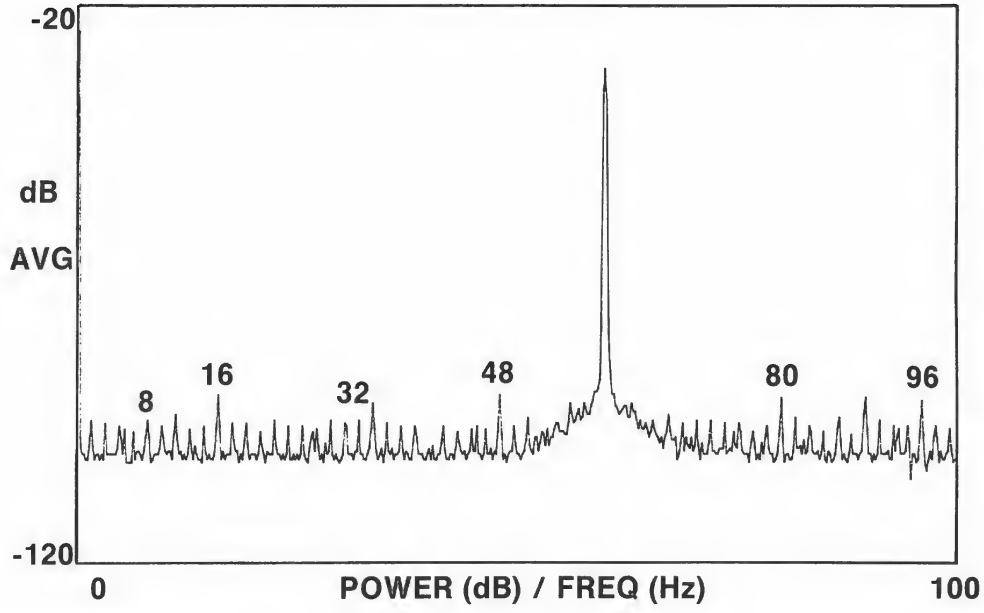

Figure 7. Spectrum (0-100 Hz) from probes on madrone (*Arbutus menziesii*). The 1.6 Hz spaced peaks show clearly. The large peak is the 60 Hz power peak which is difficult to eliminate near 60 Hz power lines. This spectrum was taken at 0543 hrs 2 August 1988 at a temperature of 10.6° C. Again this was a typical spectrum from probes in a plant. The scales are linear.

appear at frequencies $S+g_n$ or $S-g_n$ where the g_n appear to be common W-wave frequencies. Many apparent W-wave frequencies have been observed which match those commonly observed on the spectrum analyzer using the first method (two probes without a special ac source to produce beats). This beat (or heterodyne) four probe technique appears to provide an additional check on the validity of the observed W-wave frequencies. Amplitudes are often orders of magnitude larger than those observed by the simple two probe method first used. The beat method is more tedious than the direct approach since only a few frequencies usually appear with a given applied frequency but it appears to show peaks of important W-wave frequencies outside the 1.6 Hz harmonic series of the two probe method (e.g. 4, 10, and 12 Hz).

(6) The given spectra (e.g. Figures 6 and 7) result from at least eight averages on the 1201 spectrum analyzer to minimize noise. Exponential averaging was used (usually with a Hanning window) with a time constant of several seconds to several minutes (depending on the baseband used). The slow rise and fall of some of the peaks could be seen as the spectrum analyzer averaged.

(7) In initial phase tests two begonia plants (*Begonia* sp.) were displaced vertically from one another by approximately one meter. Pairs of probes were placed in each plant and the probe outputs run through high input impedance bandpass filters with center frequencies of 80 Hz (usually a large amplitude W-wave frequency). A phasemeter indicated that the 80 Hz signals obtained were related by a constant phase angle. This apparently indicated that the two 80 Hz W-wave signals were not only real but that they were causally linked (e.g. perhaps the 80 Hz signals came from a spacial (and vertical) standing W-wave pattern common to both plants).

Data Analysis and Results

If standing waves are responsible for the spacings between plant structures then both a wavelength and a frequency can apparently be

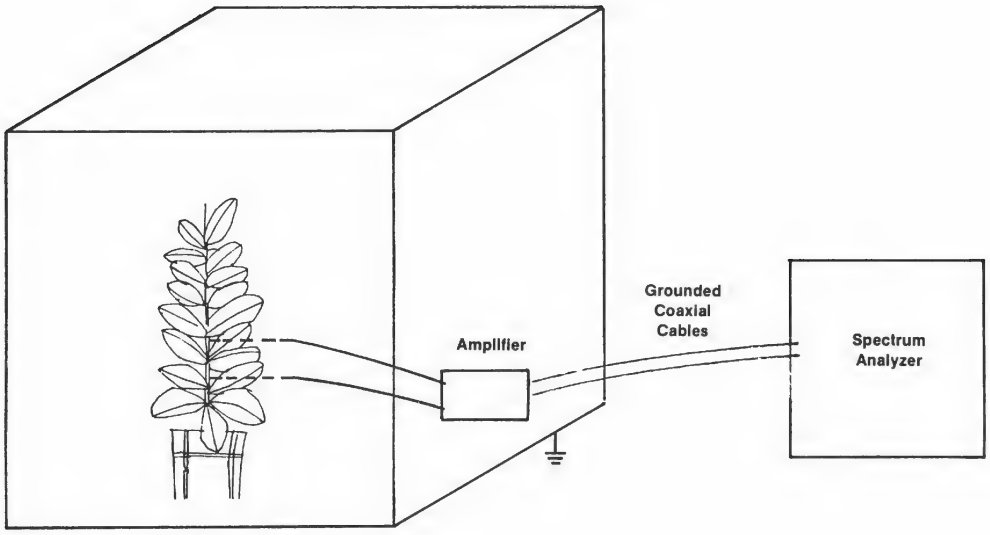

Figure 8. A diagram of one experimental setup used to show that W-waves appear in metal shields. The amplifier used was battery powered so that everything having to do with the amplifier was in the shield (aluminum box) except for the two grounded coaxial cables, going through small holes in one side of the box, taking the amplified signal to the spectrum analyzer. (See the text.)

associated with a particular spacing. As is well known for waves in general, the frequency is given as the quotient of the wave velocity and the wavelength. The *in situ* wave velocity was taken as 96 cm/sec. This velocity was chosen because a preliminary study suggested that more plant frequencies found on the spectrum analyzer matched frequencies (Hz) determined from branch spacings when this velocity was used. 96 cm/sec compares favorably with the velocity of 90 ± 6 cm/sec previously obtained from direct impulse and response measurements (Wagner 1988a,b). The frequency (f_n) of a particular spacing (using 96 cm/sec) is defined here by the following formula:

$$f_n = 96/2s_n = 48/s_n$$

where s_n is a particular spacing. The 2 in the denominator is chosen because the spacing might correlate to antinode or node spacing which is 1/2 the wavelength. The above formula was used to convert all the spacings to frequencies (Hz). Figures 2-5 are distributions of the spacings converted to frequencies in Hz. I measured the power spectrum of electrical signals from the same plants but all plants tested seemed to give the same basic spectrum.

A complete set of the spectral peaks does not always appear on the spectrum analyzer. Some peaks appear while the spectrum analyzer is averaging, then disappear and again reappear (e.g. 2.4 Hz usually seemed to show on hot afternoons). However, just by placing probes in a branch of any plant one can often obtain an almost complete set of apparent plant frequencies for the particular baseband used (e.g. Figures 6 and 7). All of the peaks shown are harmonics (integral multiples) of 0.16 Hz (or 0.02 or 0.04 or 0.08 Hz). Notice in Figure 6 that most of the peaks are spaced at 0.32 Hz, which is typical for a 20 Hz baseband. Larger amplitude peaks appear at multiples of 1.6 Hz. Even if the smaller peaks (e.g. Figure 6) fail to show in a spectrum, at least some of the 1.6 Hz series are almost always present.

After much experimentation it was decided that the most important criteria for real plant peaks on the spectrum analyzer was that they should be harmonics of 0.02, 0.04, 0.08, or 0.16 Hz, since harmonics of these particular frequencies almost always seemed to be associated with plants in my latest studies. These harmonics include the 1.6 Hz series of harmonics, which often have higher amplitudes and appear more often than other harmonics (again see Figures 6 and 7).

In Figure 7 the peaks are spaced mostly at 1.6 Hz (baseband 100 Hz). There are enough frequencies available, however, as indicated by the spectrum analyzer (e.g. Figures 6 and 7 and spectra not shown), that the distribution of branch spacings could be nearly a continuum but some of the harmonics appear to be more dominant than others. The 1.6 Hz series with their large amplitudes seem to show up in a large number of corresponding plant spacings. There probably are selection rules that determine which frequencies are dominant in setting plant spacings (it is recognized that there are many other factors involved in setting branch spacings such as environment and genetics).

Although I believe that plant spacings are set not by W-wave noise but by definite, numerous, harmonically related W-wave frequencies, it is useful to consider a criterion for peak validity when noise is present in case our assumptions are incorrect. The statistical error associated with a counting process is of the order of $\sqrt{N}$, where N is the number of counts in a particular spacing bin (interval). So in determining the validity of a plant peak, a peak which is 20 counts high would have an uncertainty of the order of $\sqrt{20}/20$ x 100 percent. If a peak is still far above the peaks in adjacent bins after $\sqrt{N}$ is subtracted from the number of spacings in that peak it can be called a real peak. This criterion not only appears to demonstrate the validity of many W-wave frequencies when frequency (Hz) is plotted versus frequency of occurrence, but if spacings are plotted versus frequency of occurrence, it becomes clear that many more of the peaks in all the distributions appear to be real by this criterion (e.g. Figure 1). I estimated that the maximum error in the frequency (Hz) in the frequency of occurrence versus frequency (Hz) plots is ± 0.1 Hz. The results, however, seem to indicate that the error is generally less than ± 0.1 Hz and probably within the possible bin error of ± 0.05 Hz since so many peaks seem to fit the 1.6 Hz series (Figures 2-5).

As an introduction to plant spacing distributions Figure 1 shows three distributions where the spacings are not converted to frequency (Hz). First notice Figure 1A where the spacing distribution is plotted for data from two apple trees. Calculations reveal that most of the larger peaks fit common W-wave frequencies when using frequency equals 96 cm/sec divided by two times the spacing (e.g. for a sample calculation take the 2 cm spacing from Figure 1A and use it as s_n in the formula $f_n = 48/s_n$ given above. This gives 24 Hz, a common W-wave frequency as revealed on the spectrum analyzer). Similarly, in Figure 1B I have a plot of spacings versus frequency of occurrence for data from five ponderosa pines. The largest peak is very apparent with a spacing of 15 cm, or 3.2 Hz using the frequency formula. In Figure 1C where the number of spacings is plotted versus spacing for concord grape, more real peaks by the above $\sqrt{N}/N$ criterion are shown than later when frequency of occurrence is plotted versus frequency (Hz) in Figure 5C.

Where growth spacings are converted to frequency it can be seen that many of the peaks repeat from plant to plant. Figure 2A, for example, shows real peaks (using the noise criterion above) at frequencies at 2.2, 6, 6.9, 8, 9.6, 12, 13.8, 15, 16, 19.2, and 24 Hz and others. Consider the validity of the 6 Hz peak. There are 15 spacings in this peak. The square root of 15 is near 4. Subtracting 4 still leaves the peak considerably higher than the adjacent peaks. The validity of the 6, 6.9, 8, 9.6, 12, 13.8, 15, 16, 19.2, and 24 Hz peaks is obvious by my criterion. Some of these peaks fit into the 1.6 series of harmonics observed on the spectrum analyzer (Figures 6 and 7) and the remainder into the 0.04, 0.08, or 0.16 series of harmonics. It appears that possible bin ($\pm .05$ Hz) and measurement errors can take care of most variations from exact fit on the spectrum analyzer peaks. In Figure 2B, some of the peaks match those of figure 2A. In Figure 2C the main peaks are: 21.9, 30, 32, 37, 40, 48, 60, and 68.6 Hz. The graphs reveal that many peaks are in the real category, as determined by our noise criteria, especially at the higher frequencies. Characteristically, it appears that, for most of the

distributions shown in Figures 2-5, those peaks at lower frequencies suggest a possible continuum of larger spacings, but if a spacing rather than a frequency (Hz) distribution is analyzed this may not be the case (Figure 1). A careful study of individual peaks suggests that no spacing is random, especially at the higher frequencies, since every peak even with only one spacing in it seems to match a 0.02, 0.04, 0.08, or a 0.16 Hz harmonic or one of the apparently more dominant harmonics of 1.6 Hz. For example, notice in figure 2C the two spacings at 80 Hz which is usually a very dominant peak on the spectrum analyzer and notice the peaks at 48 Hz in Figures 4A and 5B.

The prominence of particular peaks apparently varies not only from species to species but within the same species. Comparing spacings from plants of the same species growing in the shade and the sun it appears that shade grown plants would have larger spacings as growth is longer in the shade. This seems to be borne out by the two sets of Douglas-fir data (Figure 3A and B). Some of the main peaks of the shaded fir are at longer wavelengths (or lower frequencies: 2.3, 2.6, 3.0, and 3.4 Hz compared to 8.7, 24, 32, and 48 Hz for example) than the trees grown in the sun.

The main peaks seen in the ponderosa pine data (Figure 3C) at 1.6, 2.1, 2.4, 2.6, 3.2, 3.8, 4.8, 6.3 and 9.5 Hz (6.3 and 9.5 Hz are within 0.1 Hz of 6.4 and 9.6 Hz) show an almost perfect fit with the 1.6 Hz series from the spectrum analyzer and to other peaks that most commonly appear on the spectrum analyzer. The 2p (3.2 Hz) spacing discussed in the early data (Wagner 1988a,b) provides by far the most prominent peak here.

In Figure 4A the big leaf maple provides the largest peak at 8.8 Hz. Maple branches provide visible clues to a possible correlation between structure and wave behavior with groups of closely spaced bands often appearing just above branch whorls. These bands appear to be analogous to the standing waves that appear in small water pools connected to larger pools where a large wave has been generated. The branch whorl apparently produces a disturbance in the larger wave pattern and the results appear on the upper side of the whorl. In Figure 4B the dominant peaks are 6 and 8.8 Hz with a less dominant peak at 9.6 Hz. In Figure 4C some large peaks are at 6.4, 11, 15, 16.6, 17.2, 17.8, 19.2, 21.9, 24, 32 Hz and so on. These either fit the 1.6 series or fit the other series to probably within the possible bin error. The "signature" of syringa seems to be more complex than the signatures from other plants studied.

In sweet corn (Figure 5A) the major peaks are at 2.4 Hz and a minor peak at about 2.6 Hz which may not be real. The closest 0.32 Hz series frequency (multiple of 0.32 Hz) is 2.56 Hz and 2.4 Hz fits a 0.16 Hz series peak. Minor peaks which may not be significant are also at 3.2, 8, and 9.6 Hz which are multiples of 1.6 Hz. Figure 5B yields peaks at 9.6, 12, 13.8, 16, 19.2, 24, and 32 Hz. These peaks fit with the 1.6 series and other available frequencies. In Figure 5C the major peak is at 6 Hz (with 22 spacings) and some of the other peaks do not appear to be real. Complicated growth patterns may make it appear that spacings are less discrete. Possible variations in the *in situ* W-wave velocity during the growing season could also be a possible cause for scatter (Wagner 1988b).

When I take into account that plant frequencies can be quite small (0.04 Hz and less), and that plant frequencies can appear to be harmonics of any of the low frequencies observed on the spectrum analyzer, then all of the plant peaks from spacings fit W-wave frequencies within experimental error. A statistical correlation would appear to be meaningless for this reason. I have noticed that certain frequencies seem to be dominant, particularly those which are multiples of 1.6 Hz. Considering, for example, the number of spacing frequencies in the peaks that are labelled in Figures 2-5 (usually the peaks with the largest amplitudes) 42 percent of these spacing frequencies represent harmonics (integral multiples) of 1.6 Hz; 9.5 percent represent harmonics of 0.16 Hz (but not of 1.6 Hz); 11.7 percent represent harmonics of 0.08 Hz (but not of 1.6 Hz and 0.16 Hz); 21.1 percent represent harmonics of 0.04 Hz, and 16 percent represent harmonics of 0.02 Hz (Note: (1) There are 2300 spacings converted to frequency in the labelled peaks with about 7000 spacings represented in all the graph data; (2) Harmonics of 0.02 and 0.04 Hz are not distinguishable because the bin (interval) width used accommodates ± 0.05 Hz from the center frequency.) The large percentage of 1.6 Hz harmonics reinforces the idea that these harmonics are dominant, as suggested by the spectrum analyzer data (Figures 6 and 7).

Discussion

There are so many frequencies available in the apparent W-wave spectrum that almost any plant spacing could be allowable but it seems that certain frequencies, such as the multiples of 1.6 Hz, appear more often than others in plant spacings. Other common frequencies that appear are 4, 6, 10, 12, 60, and many others that are not integral multiples of 1.6 Hz but appear to be multiples of lower frequency subharmonics observed on the spectrum analyzer (e.g. 0.16, 0.08, 0.04, and 0.02 Hz). Since it is not clear what determines an important W-wave frequency, more study is required.

The most important observation in this study is that branch spacings often seem to be in discrete spacing groups (noise would not be expected to produce definite repeating spacings) rather than in smooth distributions and this discrete spacing would be expected from standing wave determined spacing distributions. Many of the peaks in the plant distributions repeat from plant to plant which possibly indicates the close interrelationships of plants and a common source for W-waves. Usually the major plant peaks match the major spectrum analyzer peaks shown in Figures 6 and 7, or they are harmonically related as observed earlier.

It is possible that some of the data do not fit exactly on peaks which represent W-wave frequencies because of the following hypotheses:

1) End effects. Standing wave patterns tend to set the branch spacings but with variations stemming from growing conditions. There is some evidence that wavelengths tend to be longer near ends (from unpublished data taken on salt solution filled samples) and plants grow from their ends. It is not yet clear how end effects fit into the picture but end effects are common in wave phenomena (e.g. Strutt 1945:487).

2) Errors in measurement. The spacings for the prickly lettuce data, for example, were hard to obtain because the leaves alternated from side to side along the stalk. There may be some unconscious rounding in measurement especially where there is no good reference point as in white fir. I tested this hypothesis on a white fir by covering all numbers and delineating lines except for mm marks on the measuring rule before measuring a spacing. The spacing was then marked on the rule and then the rule numbers were uncovered to see and record the spacing. This procedure was repeated until sufficient data were obtained for a comparison with data taken by the usual method. The data were then analyzed and compared to data taken without the covering precautions. This experiment indicated that there was some rounding error, but not enough to warrant retaking the data.

3) Frequency distribution slot (bin) and measurement error. Using the calculus one can derive an approximate expression that relates small changes in spacing to small changes in frequency. The relation follows:

$$\Delta s_n = -s_n^2 \, \Delta f_n / 48$$

Δs_n and Δf_n represent small changes (or errors) in spacing and frequency respectively. For example, if an interval (bin) is centered on 6 Hz (8 cm spacing) then the approximate allowable spacing error to stay within a bin of width 0.1 Hz is ± 0.7 mm. If the interval is centered on 60 Hz (8 mm spacing), however, one would have to measure within approximately ± 0.007 mm to stay within the bin. This suggests that different bins should be used for different frequency ranges. A millimeter measurement error at 60 Hz would mean an approximate frequency error of ± 7.5 Hz while a millimeter error at 6 Hz would mean an approximate frequency error of ± 0.075 Hz. The possible error introduced by the computer in taking the distributions was considered negligible.

Conclusions and Observations

These data, as reported earlier (Wagner 1988a and 1989), indicate the W-waves are apparently associated with some plant growth behavior patterns. The discrete spacing data by itself hints at the likelihood of some type of standing wave function with frequencies repeating on individual plants and from plant to plant. A comparison of spectrum analyzer data, where actual frequencies are measured, with spacing frequencies calculated with a wave speed of 96 cm/sec, reinforces the idea that W-waves explain the discrete plant spacings. This invites further investigation into the source(s) and function of W-waves.

The number 1.6, which appears here, is close to the *golden ratio* (Dixon 1989). Perhaps W-waves are related to the Fibonacci numbers as they are manifested in plants. W-waves might

also be involved in other natural phenomena, such as in the formation of quasicrystals, where the *golden ratio* appears.

Acknowledgments

The author wishes to thank John Salinas of Rogue Community College for his assistance in analyzing data. I also would like to thank Dr. Alan Streater of the Southern Oregon State College physics department for his comments on this paper. I am grateful to my wife Claudia for her assistance in taking data.

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Received 12 October 1988
Accepted for publication 13 October 1989

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The Effects of *Trichoderma* spp. Isolated from Burned and Non-Burned Forest Soils on the Growth and Development of *Armillaria ostoyae* in Culture

Abstract

Several species of the fungus *Armillaria* cause root disease in a variety of plants worldwide. We wished to see if prescribed fire would alter the rhizophere to favor the soil fungus *Trichoderma* spp. which has been shown to be strongly antagonistic to *Armillaria,* the fungus that causes Armillaria root disease in conifer forests. We found that isolates of *Trichoderma* spp. obtained from burned and non-burned soils beneath a ponderosa pine forest in central Oregon were strongly antagonistic to *Armillaria ostoyae* in culture. Filter-sterilized filtrates of these *Trichoderma* isolates inhibited rhizomorph formation by *A. ostoyae* and reduced its growth on solid media. Isolates of *Trichoderma* represented about 20 percent of the fungi recovered from burned and non-burned soils; however, the isolates obtained from burned soils were more antagonistic to *A. ostoyae* than were the isolates obtained from non-burned soils. There was also a difference in the species of *Trichoderma* recovered from burned and non-burned soils. Of the eight isolates of *Trichoderma* that were identified, *T. citrinoviride* occurred more frequently in burned soils (3 of 4 isolates), whereas *T. harzianum* was more common in non-burned soils (3 or 4 isolates). *Trichoderma citrinoviride* was more antagonistic to *A. ostoyae* than was *T. harzianum.* These results suggest that the judicious use of fire may aid efforts to control Armillaria root disease in pine forests.

Introduction

Several species of the fungus *Armillaria* cause root disease on a wide range of plant hosts throughout the world (Raabe 1962, Wargo and Shaw 1985). Both the fungus and the root disease it causes are common in coniferous forests and plantations of the Pacific Northwest (Hadfield *et al.* 1986) and economic losses can be substantial (Smith 1984, Wargo and Shaw 1985).

Several *in vitro* and *in situ* studies have demonstrated that various soil fungi are antagonistic to *Armillaria* (Shaw and Roth 1978). Recently, Munnecke and others (Munnecke *et al.* 1973, 1981) showed that the soil fungus *Trichoderma* spp. is responsible for the death of *Armillaria* mycelia on citrus trees after *Armillaria* has been "stressed" by fumigation with carbon disulfide. Similar stress to *Armillaria* can be achieved by heating and drying (Munnecke *et al.* 1981).

An inability to maintain effective populations of organisms antagonistic to *Armillaria* under normal field conditions is considered to be the main factor limiting successful biological control of this root disease in forests (Shaw and Roth 1978). Because prescribed fire can influence the population of antagonistic microorganisms in soil (Margaris 1977, Parmeter 1977, Lucarotti *et al.* 1978), judicious use of fire may aid in efforts to control root disease; for example, a controlled burn produced a temporary reduction in the population of *Phytophthora cinnamomi* Rands in soil (Hardison 1976). The reduction was attributed to a shift in the soil microbial balance rather than to direct killing of the pathogen by heat.

This strategy for disease control is similar to that used by Munnecke *et al.* (1981) in which soil fumigants indirectly affected *A. mellea* (Vahl.) Quel by favoring the antagonistic fungus *Trichoderma.* Although such control is theoretically feasible (Munnecke *et al.* 1973, 1981), additional research is needed before procedures aimed at modifying populations of soil organisms antagonistic to *Armillaria* can be implemented as effective disease control measures, particularly in forests.

In this study, we evaluated the effects of prescribed fire in a ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forest on the soil population of *Trichoderma* spp. We then evaluated the effects of selected *Trichoderma* spp.,

isolated from burned soils or non-burned soils, on the growth and development of *A. ostoyae* (Romangn.) Herink.

Materials and Methods

Field Studies

Study area description

Burned and non-burned plots were located in a stand of ponderosa pine in the Pringle Falls Experimental Forest about 48 km (30 miles) south of Bend, Oregon. Armillaria root disease occurs throughout the area (Adams 1974). The topography has a gentle slope with a southeast exposure. Soil is of the LaPine pumice series and vegetation is of the Volland Ecoclass (CP-S2-17—ponderosa pine/bitterbrush/manzanita/fescue (Franklin and Dyrness 1969). About 0.4 ha (1 acre) was burned; the fuel load on the site before burning was moderate. Burning conditions and time are described elsewhere (Reaves 1985).

Isolation of Trichoderma *from soil*

A total of 24 pits each measuring 30 cm long, 25 cm wide, and 50 cm deep, were dug during the summer months in burned (12 pits) and non-burned (12 pits) areas. Pits were randomly located within these areas at points over 20 m apart. Soil removed from all pits had similar, but low, moisture content (16% to 20%) (Reaves 1985).

Fungi were collected from these pits by horizontally inserting three Mueller-Durrell (M-D) tubes (Mueller and Durrell 1957), each with eight entry points, in every pit (Figure 1). The tubes contained peptone dextrose agar (Martin 1950) and were inserted at 5-, 10-, and 20-cm depths after burning (4 pits per time period at 5, 30, 60 days). Similar pits, dug in adjacent non-burned areas with the same sampling design for M-D tubes, served as controls. Thus, for each of three soil depths and three times of burning there were 32 M-D tube entry points for sampling fungi (288 total), and a similar number from pits in the non-burned, control plots.

Tubes remained in the pit walls for five days. All pits were left open during sampling, except for those sampled five days after burning where pits and the surrounding area were reconstructed as closely as possible to the original state. After the sampling period, all tubes were removed from pits. Fungal hyphae, which were visible to the unaided eye at all entry points, were aseptically removed from each entry point with a sterile scalpel and placed on solid malt extract medium (MEM) which is defined below. Fungal cultures were obtained from all 576 entry points. These cultures (288 from non-burned and 288 from burned soils) were incubated under continuous incandescent light and ambient room temperature

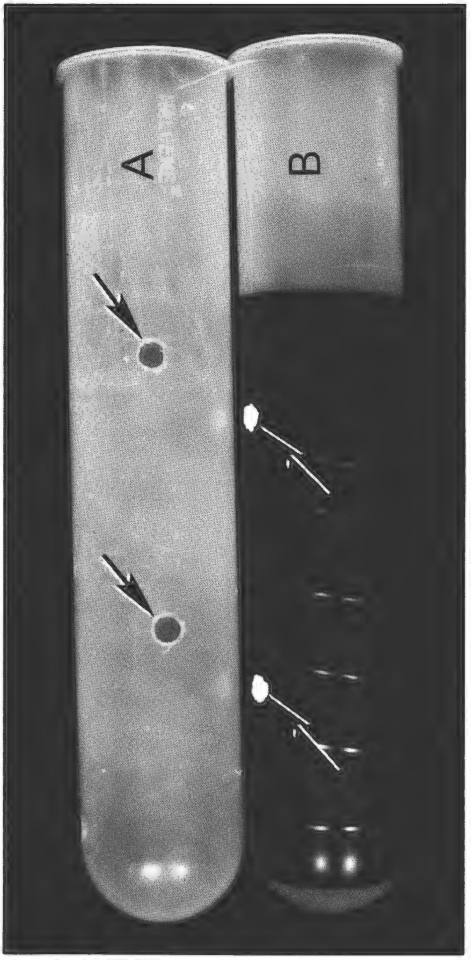

Figure 1. Mueller-Durrell tubes used for isolation of *Trichoderma* from soil. (A) Unwrapped tube showing holes (arrows) for entry of fungal hyphae from soil. Two of the eight holes are visible. (B) Tubes were wrapped with electrical tape before placing in soil. Holes were punctured through the tape with sterile pin to allow for fungal entry (arrows).

for 10 days to aid in formation of conidia. Most cultures were examined only macroscopically and based on colony characteristics, were determined to be isolates of *Trichoderma* or unknown fungi. Eight of the *Trichoderma* isolates were examined microscopically to determine species (J. Bissett pers. comm., Biosystematics Research Institute, Ottawa, Ontario, Canada).

Laboratory Studies

Fungi and media

The isolate of *A. ostoyae* used in this study was obtained in 1982 from a mycelial fan beneath the bark of dead ponderosa pine tree near Bend, Oregon. This isolate was identified as *A. ostoyae* by the authors using methods outlined by Wargo and Shaw (1985), Morrison *et al.* (1985), and by D. Morrison (pers. comm., Canadian Forestry Service, Victoria, British Columbia, Canada). *Armillaria ostoyae* was maintained on a solid medium which tonained 30 g malt extract, 20 g dextrose, 20 g agar, and 5 g bacto-peptone per L of distilled water. Medium pH was adjusted to 5.6-6.0 with 1.0 N HCl prior to sterilization in an autoclave. Liquid media had the same ingredients, minus agar. These media are designated as solid and liquid malt extract medium (MEM). Water agar medium (WAM) had 20 g of agar in 1 L of distilled water.

Filtrate collection

Isolates of *Trichoderma* from burned (4 isolates) and non-burned (4 isolates) plots were grown in plastic petri dishes (100 mm x 15 mm), each of which contained approximately 20 ml of MEM, under continuous incandescent light until conidia formed. Each plate was then flooded with 25 ml of sterile distilled water and agitated by hand for two minutes to dislodge the conidia. Conidial suspensions were diluted to approximately 1.0 x 10^7 conidia/ml (Elad *et al.* 1982) and 0.25 ml of this suspensions was added to a 500-ml Erlenmyer flask containing 250 ml of liquid MEM and incubated for five days at ambient room temperature. After incubation, the cultures were filtered through Whatman's No. 1 filter paper and then through 0.20-μm Millipore filter to obtain filter-sterilized filtrates. Microscopic examination verified that filtrates were free of conidia.

We determined, by the O-toludine Method (*Sigma Chemical Co.* 1980), that the isolates of *Trichoderma* spp. used 4 mg dextrose/ml of MEM during this 5-day growth period. To compensate for this use of dextrose by *Trichoderma* while growing in liquid MEM, an additional 4 g of dextrose was added to each liter of MEM prior to mixing it with the *Trichoderma* filtrates. The pH of all filtrates of *Triochoderma* was adjusted to 5.8-6.0 (equal to that of the filtrate-free MEM) before mixing with sterilized MEM (1:1, v/v).

Growth of A. ostoyae *on MEM amended with* Trichoderma *filtrates*

Eight isolates of *Trichoderma,* four from burned and four from non-burned soils, were randomly selected from those obtained during the field study.

Mycelial discs (4 mm diam.) of *A. ostoyae* from 15- to 20-day-old cultures grown on WAM were placed on petri dishes (10 dishes for each *Trichoderma* isolate in each of 2 replications) containing MEM amended with filtrates (1:1, v/v) from one of the eight isolates of *Trichoderma,* and incubated in the dark at 25°C for 21 days. After incubation, colonies of *A. ostoyae* were scored for the presence or absences of rhizomorphs. Agar was then removed from around the colonies by boiling in water for 10 minutes. The colonies were blotted on filter paper, and dried at 90°C for 72 hours, and colony dry weights (CDW) were then determined. Similar methods have been used to obtain dry weights of *Armillaria* colonies grown on solid medium (Shaw 1975, 1985, Cheo 1982, Reaves *et al.* 1984). In addition, differences in appearances of colonies of *A. ostoyae* grown on solid MEM containing autoclaved or non-autoclaved filtrates of *Trichoderma* were observed, but not quantified.

Statistical Analysis

All data were subjected to an analysis of variance followed the Student Newman-Kuels multiple range test (Snedecor and Cochran 1969). All differences were judged to be significant at $P \leq 0.05$.

Results

Field Studies

Isolation of Trichoderma *from soils*

Sixty-nine isolates of *Trichoderma* spp. were recovered from the 288 tube entry points in

burned plots, and 46 from the same number of sampled entry points in non-burned plots Thus, about 20 percent of the fungal flora obtained from either bunred or non-burned soils were isolates of *Trichoderma.*

Trichoderma isolates were recovered at 5, 30, and 60 days after prescribed burning (and in non-burned plots). In burned plots, however, the number of *Trichoderma* isolates recovered 5, 30, or 60 days after burningw as considerably greater at 10 cm than at depths of 5 or 20 cm (Table 1). In addition, the number of *Trichoderma* isolates obtained from the 10-cm depth at each isolation time was consistently greater on burned plots (Table 1). Three of the four isolates randomly selected for identification from burned plots were *T. citrinoviride* Bissett (the other was *T. harzianum* Rifai) but three of the four isolates from non-burned plots were *T. harzianum* (the other as *T. citrinoviride*).

TABLE 1. Recovery of *Trichoderma* isolates from soil pis after 5, 30, and 60 days in non-burned and burned plots.[a]

	Non-burned			Burned			
	Days[b]						
	5	30	60	5	30	60	
	Number of isolates recovered[c]						
Soil depth (cm)							Totals
5	9	4	3	9	3	3	31
10	11	4	3	20	10	9	57
20	5	3	4	9	5	2	28
Totals	25	11	10	38	18	14	116

[a]Mueller-Durell tubes used for *Trichoderma* isolation were placed in pits before burning and removed 5 days after burning.

[b]Number of days after burning that fungal samples were taken. The sampling period was 5 days.

[c]Each number in the table represents the number of *Trichoderma* isolates recovered from 32 samples of soil fungi collected at that soil depth and time of sampling. The total number of fungal cultures (*Trichoderma* and unknown fungi) recovered from both burned and non-burned soils was 576.

Laboratory Studies

Effects of Trichoderma *filtrates on the growth of* A. ostoyae

Armillaria ostoyae grown on filtrate-free MEM had significantly greater CDW than when grown on solid MEM amended with filtrates of seven of the eight isolates tested from burned or non-burned plots (Table 2). In addition, *A. ostoyae* grown on solid MEM amended with filtrates from three of the four isolates from burned plots (*T. citrinoviride* isolates Nos. 5, 6, 7, Table 2) had lower CDW than those amended with filtrates from three of four isolates from non-burned plots (*T. harzianum* isolates Nos. 1 and 3 and *T. citrinoviride* isolates No. 2, Table 2). These differences were consistent in both replications but significant for all three isolates only in replication No. 1 (Table 2).

TABLE 2. Dry weight and rhizomorph development by *A. ostoyae* on solid medium amended with filtrates of *Trichoderma* spp. isolated from burned (B) or non-burned (NB) plots.

Trichoderma isolate No., species, and origin	Replications 1	Replications 2
	Dry weight and rhizomorph development[x,y,z]	
Filtrate-free MEM (control)	399 ± 98[a] +	306 ± 43[a] +
1. *T. harzianum* (NB)	62 ± 17[b] +	94 ± 8[b] +
2. *T. citrinoviride* (NB)	88 ± 13[b] +	91 ± 5[b] +
3. *T.harzianum* (NB)	317 ± 95[a] +	116 ± 18[b] +
4. *T. harzianum* (NB)	19 ± 7[c] —	67 ± 5[b] |
5. *T. citrinoviride* (B)	14 ± 5[c] —	23 ± 2[c] —
6. *T. citrinoviride* (B)	19 ± 9[c] —	64 ± 7[b] |
7. *T. citrinoviride* (B)	16 ± 3[c] —	73 ± 5[b] |
8. *T. harzianum* (B)	130 ± 10[d] +	92 ± 9[b] +

[x]Mean and standard error, 10 replications.

[y]Mean values followed by different letters in columns or rows differ significantly ($P \leq 0.05$) as determined by the Student Newman-Kuels test.

[z](+), indicates that rhizomorphs developed well beyond the inoculum plug, (—), indicates that rhizomorphs were completely absent; and (|), indicates that rhizomorph initials were within the confines of the colony.

Rhizomorphs did not form in cultures amended with filtrates from the three isolates of *T. citrinoviride* identified from burned plots; however, rhizomorphs did form in cultures amended with filtrates from three of the four isolates obtained from non-burned plots (Figure 2). Also, whereas pseudosclerotia were complete in controls, they formed only partially in cultures amended with any filtrates. Thus, even though filtrates from most isolates of *Trichoderma* inhibited the growth of *A. ostoyae* in culture, the isolates identified from burned plots were generally more inhibitory than those than those from non-burned plots. Rhizomorphs did not form in solid MEM amended with autoclaved *Trichoderma* filtrates.

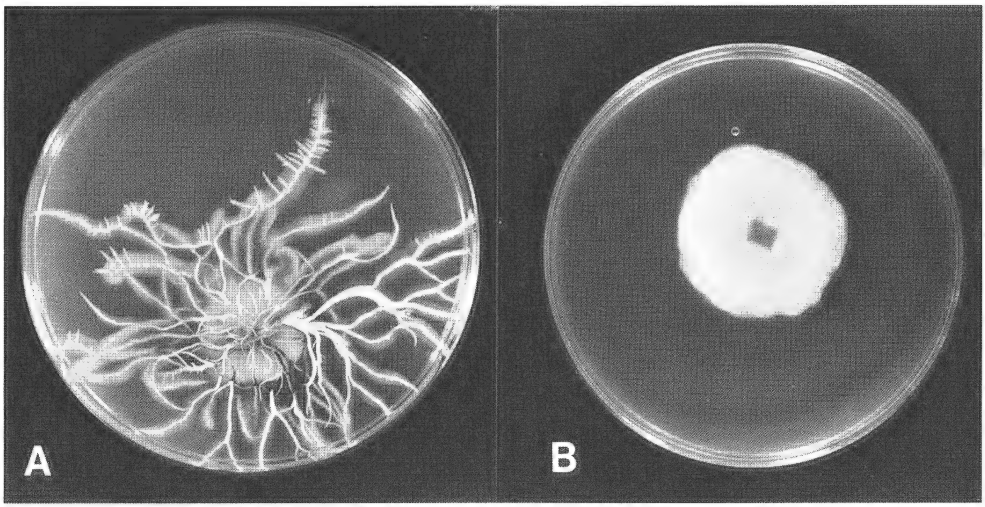

Figure 2. Bottom view of typical colonies of *A. ostoyae* after 21 days growth. (A) Growth of *A. ostoyae* on solid malt extract media without filtrates (control). (B) Growth of *A. ostoyae* on solid malt extract media amended with filtrates of *T. citrinoviride*.

Discussion

Filtrates obtained from cultures of eight different isolates of *Trichoderma* all reduced the growth of *A. ostoyae* in culture. *Trichoderma viride* Per. ex Fr. had a similar reductive effect on the growth of *A. ostoyae* in liquid culture (Reaves 1985). This effect on solid MEM can be at least partially attributed to the sparse development or complete absence of rhizomorphs. Antagonism appears to be caused by a diffusible metabolite(s) that suppressed, and sometimes stopped, the production of rhizomorphs by *A. ostoyae*. The fact that autoclaved filtrates of *Trichoderma* isolates inhibited growth of *A. ostoyae* illustrates that the metabolite(s) is not an enzyme, because the temperatures reached during autoclaving (ca. 115°C) should have denatured any enzymes present.

Colony dry weights of *A. ostoyae* were generally lower when the fungus was grown on solid media amended with filtrates of *Trichoderma* isolated from burned soils than when amended with filtrates of *Trichoderma* from non-burned soils. This phenomenon appears to be related to the species of *Trichoderma* present. Fire, or ash therefrom, may have altered soil conditions in a manner that favored particular species of *Trichoderma*. For example, three of the four isolates we identified from burned soils were species of *T. citrinoviride*, whereas three of the four isolates identified from non-burned soils were *T. harzianum*. *Trichoderma citrinoviride* was more antagonistic to *A. ostoyae* than *T. harzianum*. Thus, fire may aid in elevating soil populations of *Trichoderma* spp. that are highly antagonistic to *Armillaria*.

Interestingly, leachates with a large cation component (Grier 1975) from ashes of pine litter increased the dry weight of conidia of *T. viride* in culture, an increase that was proportional to the concentration of ash leachates (Reaves *et al.* 1984). This effect of ash may be important to the potential use of prescribed fire as an aid to disease control, as soil populations of *Trichoderma* spp. would have to be increased and maintained at a high level to affect the growth of *Armillaria* rhizomorphs in soil (Shaw and Roth 1978).

In summary, prescribed fire increases the concentration of cations (leached from the ash layer) in soil (Reaves 1985). These cations have negative effect on the *in vitro* growth and development of *A. ostoyae* (Reaves *et al.* 1984). However, leachates from the ash layer accumulated after fire have a positive effect on *Trichoderma* spp. which, in turn, reduce the growth and rhizomorph formation by *A. ostoyae*. Together these components could enhance opportunities

for integrated biological control of Armillaria root disease through judicious use of fire. Similar studies should be conducted over a broader geographical range to test the effectiveness of prescribed fire as a means of elevating soil populations of *Trichoderma* spp. that are antagonistic to *Armillaria.*

Acknowledgments

The authors thank Dr. John Bissett for assistance with the identification of *Trichoderma* isolates and Timothy Max for assistance with the statistical analysis.

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Received 20 March 1989
Accepted for publication 3 August 1989

This paper is adapted from portions of a dissertation submitted by Jimmy L. Reaves in Biology, Graduate School of Arts and Sciences, Atlanta University, Atlanta, Georgia.

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Causes of Basal Scars on *Chamaecyparis nootkatensis* in Southeast Alaska

Abstract

Scars on the lower boles of Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) trees are common in some unmanaged forests in southeast Alaska, but their cause has not been determined. The association of these basal scars with an extensive decline and mortality of unknown cause that affects Alaska yellow-cedar also has been unclear. Data from ground transects indicate that on Baranof and Chichagof Islands over one-half of the Alaska yellow-cedar trees in some stands are scarred, even though other tree species are not affected. Scars generally face upslope, do not girdle the entire circumference of the bole, average 1.5 m in height, and are most common on the best drained, most productive sites. These productive sites lack cedar decline. Callus tissue slowly forms over these basal scars, but decay develops in the wood, reducing wood volume in the valuable butt logs. Fungi that occur on scars of varying ages are described. Recent scars consistently have teeth marks in the exposed wood—evidence that bears cause this damage. Such basal scars are common on islands in southeast Alaska inhabited by brown bears (*Ursus arctos*), but not on islands inhabited by black bears (*Ursus americanus*). Cedar decline occurs on several islands not inhabited by brown bears and where cedars are not scarred. Scarring was no more common on dying versus healthy cedars or in declining versus healthy stands; thus, basal scars are not a significant factor in decline of Alaska yellow-cedar.

Introduction

Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), a long-lived, valuable tree species in southeast Alaska, has been suffering from an extensive decline and mortality that now covers more than 150,000 hectares of primarily unmanaged and remote forest (USDA Forest Service 1988). This forest decline began about 1880 (Hennon 1986), but the primary cause remains a mystery (Frear 1982, Shaw *et al.* 1985, Hennon 1986). In the course of our recent investigations on the causes and epidemiology of decline, we noted the common association of basal scars with dead and dying cedars.

Scars are common on the lower bole of Alaska yellow-cedar trees in some areas of southeast Alaska (Anderson 1959), including some areas where decline and mortality is severe (Shaw *et al.* 1985). The involvement of scars in causing tree death is not known. Ruth and Harris (1979) noted that bears may cause scars on cedar, but this has not been substantiated.

Presently, there is no information on tree species affected by scarring, fungi and decay in scars, the geographical extent of scarring, or, except for the idea proposed by Ruth and Harris, what may be causing these tree scars. The objectives of this study were to 1) describe characteristics of scars, tree species affected and tree responses to scarring; 2) determine the cause(s) of scarring; and 3) determine if there is an association between the occurrence of scarring and the decline and mortality of Alaska yellow-cedar.

Materials and Methods

Most studies were conducted on Chichagof and Baranof Islands northeast of Sitka at Peril Strait, Slocum Arm, and Kennel Creek (Figure 1). Studies were also conducted near Control Lake on Prince of Wales Island and Rainbow Falls on Wrangell Island. The occurrence and size of basal scars were noted for 779 Alaska yellow-cedars as well as for other tree species (western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), mountain hemlock (*T. mertensiana* (Bong.) Carr), and shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*)) present on 280 plots along 21 survey lines on Chichagof and Baranof Islands. Survey lines

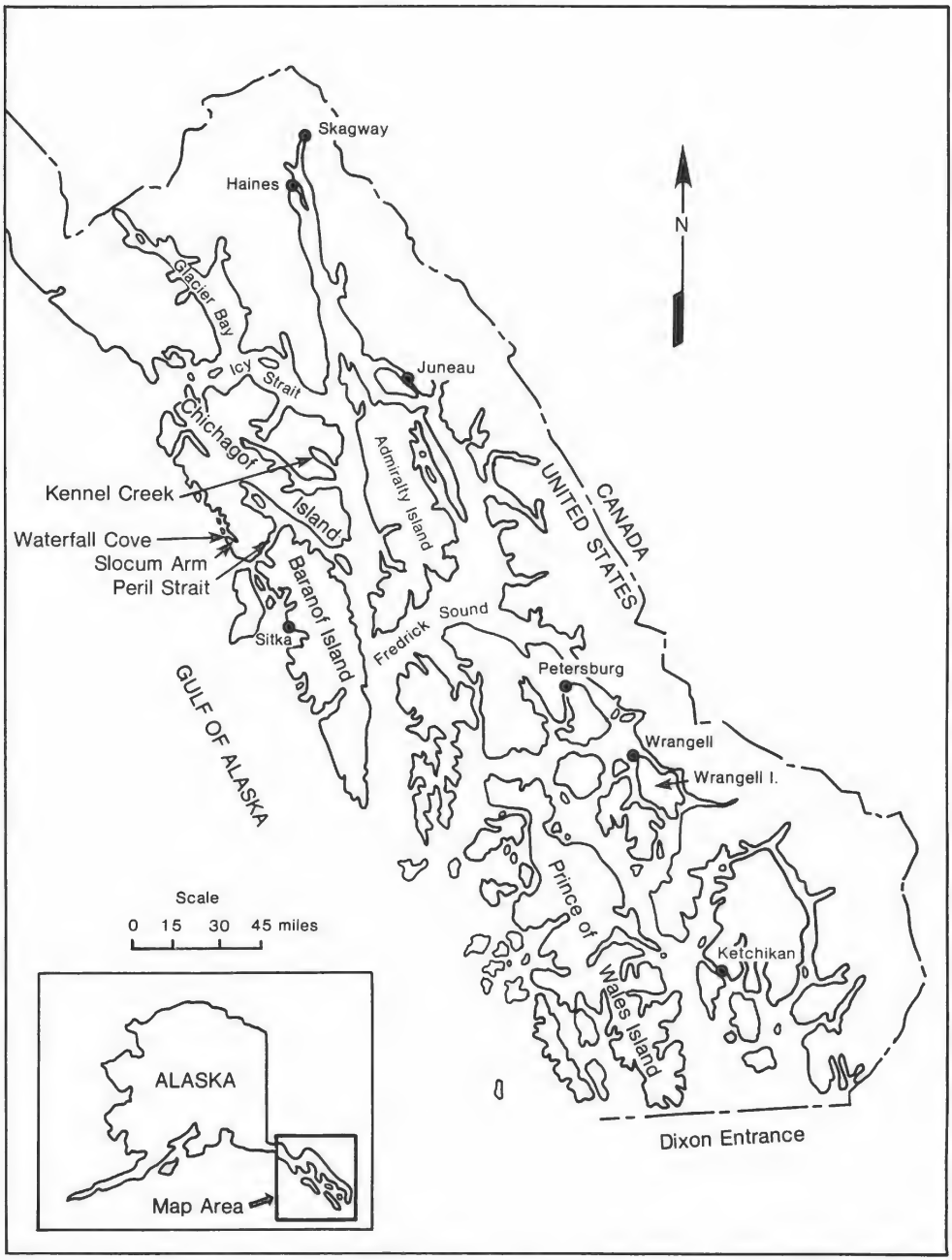

Figure 1. Location of study sites in southeast Alaska.

were designed to pass through and beyond stands with noticeable cedar decline and mortality. Lines commonly began at beaches and ran directly upslope with plots every 50 m until two or more plots were located in "healthy" stands that lacked concentrations of dead and dying trees. Individual trees were selected on each plot with a 3- or 6-m^2/ha basal area factor prism. Most sampling (16 lines) was along Peril Strait, but survey lines were also located in Slocum Arm near Waterfall Cove (one line) and Kennel Creek (four lines), both on Chichagof Island (Figure 1). Scar heights and orientation with slope were measured from an additional 490 Alaska yellow-cedars at three sites at Peril Strait. Heights of 24 fresh scars with noticeable bite marks were measured at Peril Strait to determine how they compared to the heights of the primarily older callusing scars.

Sampling was also conducted further south within the natural range of western redcedar (*Thuja plicata* Donn) on Prince of Wales Island (64 plots with 163 Alaska yellow-cedars) and Wrangell Island (80 plots with 421 Alaska yellow-cedars). In total, 1853 Alaska yellow-cedar trees were examined.

A Chi-square analysis ($P = 0.05$) was used to test if the incidence of scarring 1) differed with location (Peril Strait, Slocum Arm, Kennel Creek, Prince of Wales I., and Wrangell I.) (Fleiss 1981), 2) differed in the Peril Strait area for live cedar trees located within stands suffering from decline ($\geq 33\%$ basal area dead) compared to live cedars within relatively healthy stands ($< 33\%$ basal area dead), and 3) differed in the Peril Strait area for dying cedars (crowns yellow or thin) compared to healthy-appearing cedars. Frequency distributions were drawn for scar height and orientation, and the latter was tested using the Rayleigh test (Batschelet 1965) ($P = 0.05$), a Z statistic which tests for distribution around a circle, to determine if scars faced any particular direction.

An understory plant ordination was used to determine if the occurrence of scarring was correlated with differences in forest communities. The dominance or absence of 55 plant taxa (Hennon 1986) were recorded on each of the 280 plots in Peril Strait, Slocum Arm, and Kennel Creek. Dominance rating included five categories: nearly pure in its layer ($> 50\%$ cover), dominant (25-50%), common (5-25%), rare (0-5%), and absent. A gradient of plot scores was calculated from a computer ordination technique—Detrended Correspondence Analysis (DECORANA), which generates axes that represent gradients of plant species' distribution (Hill and Gauch 1980, Gauch 1982). Based on field observations of the distribution of these plants and their associated overstory, these plot scores from the first and dominant axis represent the gradient from bogs to plant communities with better drainage (Hennon *et al.* 1984). DECORANA plot scores from this first axis using 232 plots (some plots were dropped because cedar was absent or fewer than two trees were alive) with a total of 679 cedar trees were plotted against the proportion of Alaska yellow-cedars with basal scars.

In Peril Strait, three Alaska yellow-cedars with scars were dissected transversely with a chain saw to allow for examinations of decay characteristics and tree responses to wounding. Single discs were cut from the boles of 15 other Alaska yellow-cedars with basal scars and similarly examined.

Fruiting bodies of fungi were collected from fresh and old basal scars to determine the mycoflora present on scars of different ages. Physical characteristics of these scars (e.g., depth of wound in relation to amounts of callus tissue, condition of exposed wood, and presence of fungal fruiting bodies) were also recorded. In addition, 113 attempted isolations were made from basal scars (mostly less than 5 years old) onto two types of artificial sterile media: potato dextrose agar and 1.5 percent malt extract agar (with 2 ppm benomyl). Microscopic and cultural characteristics of collected and isolated fungi are reported elsewhere (Hennon 1986).

Results

Occurrence of Scars

Basal scars were present on 49 percent of the Alaska yellow-cedar trees sampled on Chichagof and Baranof Islands. Scars were common at Waterfall Cover (62%) and along Peril Strait (51%) but were significantly ($P = 0.05$) less frequent at Kennel Creek (16%) and absent on cedars on Prince of Wales and Wrangell Islands. At Peril Strait, at least 30 percent of the Alaska yellow-cedar trees from each of the 16 transects had scars. Except for trees less than 10 cm dbh, all size classes were scarred. Scar incidence at Peril Strait did not differ significantly between live cedars within healthy stands (51% scarred)

and those in declining stands (50% scarred) or between healthy (51% scarred) and declining (49% scarred) individual trees.

Scars on Alaska yellow-cedar had a significant (P = 0.05) upslope orientation at each of the three sites where orientation was measured. Most scars were about 150 cm tall, but taller scars were also common (Figure 2).

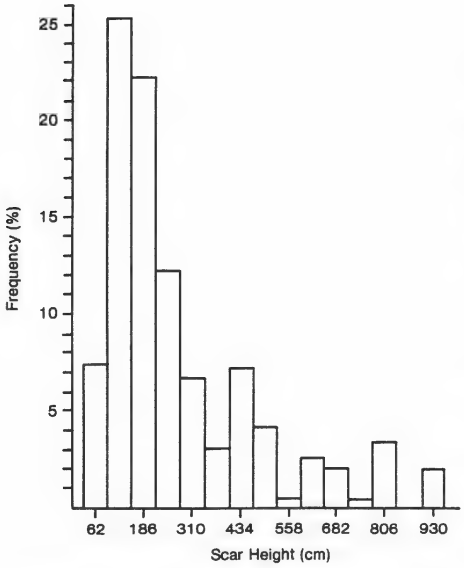

Figure 2. Frequency distribution of scar heights on 229 Alaska yellow-cedar trees located near Peril Strait, Alaska.

Marks, apparently made by animals, were present on nearly all fresh scars (Figure 3 A,B). Heights of the 24 scars with bite marks averaged 164 ± 72 cm (range = 26-270 cm). The actual teeth marks had an average height above ground of 44 ± 20 cm (range = 12-88 cm). Some Alaska yellow-cedar trees had several adjacent basal scars, usually with different depths of callus folds as if they occurred at different times. Scars were generally most common in better drained forest types, although they were found on Alaska yellow-cedars in all communities (Figure 4). Very few basal scars were found on other conifers, and the few observed did not resemble the scars on Alaska yellow-cedars in size or shape.

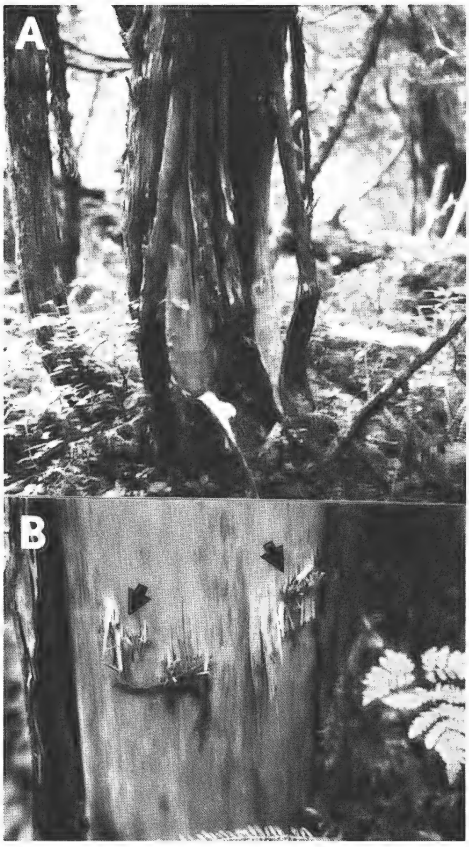

Figure 3. A), Fresh basal scar on Alaska yellow-cedar caused by brown bears; B), note the teeth marks (arrows) on exposed wood caused by bears tearing bark from these trees.

A different type of basal scarring was found on 11 Alaska yellow-cedars along Peril Strait. These scars were distinguishable from others by the presence of a distinct horizontal cut across the top, and often the bottom, of the scars; they were also taller than the scars described above (Figure 5). These scars were on some of the largest Alaska yellow-cedars in the stand, almost all were found close to the beach, and scars did not show any trend for occurring on the upslope side of trees.

Responses to Wounding

The first noticeable tree response was evident the spring following wounding when callus tissue

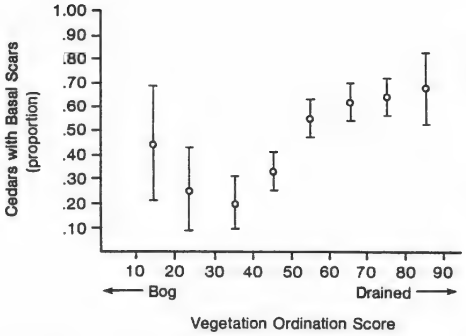

Figure 4. Proportion of Alaska yellow-cedars with basal scars from 8 intervals of understory vegetation gradient from bog (low scores) to better drainage (high scores). Vegetation ordination scores based on DECORANA from 232 plots along 16 survey lines with 679 Alaska yellow-cedars growing along Peril Strait on Baranof and Chichagof Islands, Alaska. Bars are standard errors of the sample proportion mean.

began to develop along the sides, bottom, and top of the wound. Cross sections cut through tree wounds showed that changes in the sapwood on the edges of the wound occurred within several years. Sapwood exposed by the wound was dead (Figure 6), but live sapwood adjacent to both sides of the wound turned bright yellow, a color more intense than in normal Alaska yellow-cedar heartwood. As callusing sapwood slowly engulfed the sides of the wound, it also developed this bright yellow color. Cross sections cut through older wounds suggested that these reactions confined decay to a narrow crescent-shaped band of the sapwood exposed during the scarring event, but decay eventually developed in surrounding wood in some of the oldest (50+ years) scars.

Fungi on scars

Stain and decay were not confined in the wood above scars. One decay arc extended 3.2 m above the top of the scar, with advanced decay occurring in all but the top 0.2 m. *Leptographium* sp., probably saprophytic on Alaska yellow-cedar (Hennon *et al.* 1984), was the fungus most frequently isolated from the tops of these stain columns.

Dead sapwood within the wound changed from its original near-white color to a tan, and then to greenish black or black within several

Figure 5. Large basal scar caused by humans collecting bark from Alaska yellow-cedars. Note the horizontal cuts along the top and bottom of the scar.

years after scarring. *Leptographium* sp. was the most common fungus isolated from the stain when tan-colored. Fungi isolated from the black-colored stain included the following: *Sporidesmium* sp., *Phialophora* sp., *Mycelium radicis atrovirens,* and *Leptographium* sp.

Phloem (inner bark), freshly exposed by wounding, was bright and creamy white in color. This phloem, which was stripped away from the sapwood, but often still attached at the top and bottom of the wound, changed color to a cinnamon brown within a few hours after wounding.

Several Alaska yellow-cedars with very fresh scars, initially still with white phloem, were revisited one and two years after being scarred;

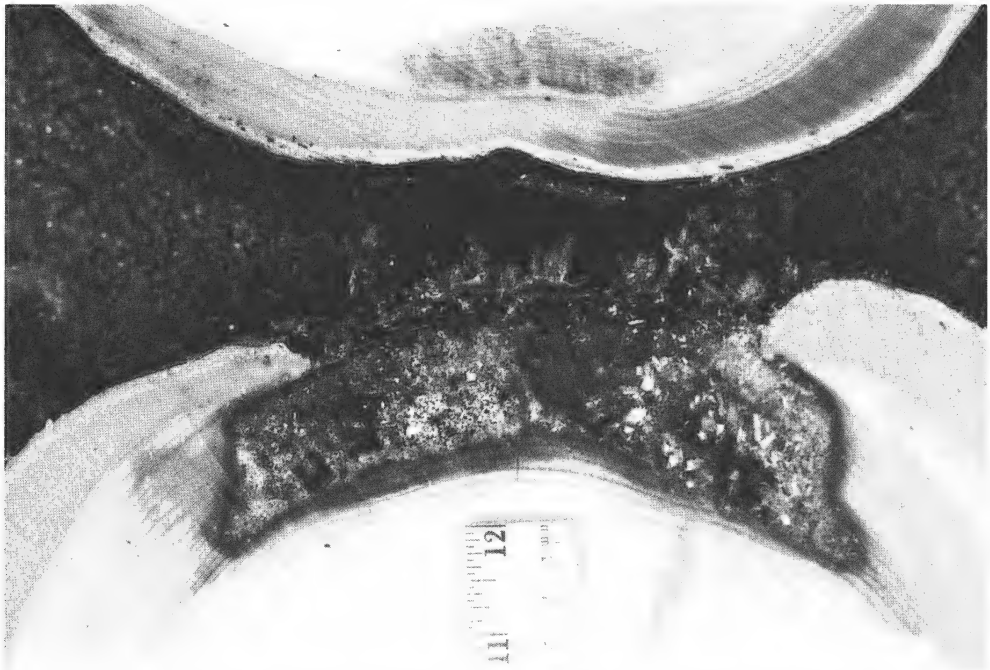

Figure 6. Cross sections through an Alaska yellow-cedar tree with a basal scar. Below: note the callus tissue that grows over the wound and the relative restriction of decay to the sapwood killed during the scarring event. Above: note the incipient decay in this section, which was removed from the bole above the scar.

Ceratocystis sp. and *Pistillaria* sp. were the only fungi found sporulating directly on these young scars. *Ceratocystis* sp. was found only on one-year-old scars and only sporulated on the bark and sapwood where these two tissues were killed, but not permanently separated. After a year or two, the stripped bark fell off, leaving the sapwood fully exposed.

The diversity of fungal species increased as the scars aged, reached a peak as the sapwood began to decay, but decreased once most of the sapwood became thoroughly decayed and eventually rotted away (Table 1). Fungi found on older scars were also found growing as saprophytes on other dead tissues of Alaska yellow-cedars (e.g., dead twigs, limbs, and boles). None of the fungi collected or isolated from basal scars appears to be capable of causing these scars or killing trees (Hennon *et al.* 1984).

Discussion

Scars with teeth marks were almost certainly made by brown bears (*Ursus arctos*). These marks in sapwood are made by canine teeth as the bears attempt to pull bark from trees with their mouths (J. Schoen, AK Dep. Fish and Game, pers. comm.). Hair of brown bear was found in some recently produced scars. The bite marks produced when bears pull bark away were the only obvious marks on the scar; once bark was pulled away, bears did not use their teeth or tear at exposed wood with their claws. Perhaps bears lick exposed phloem which contains concentrations of sugars (primarily sucrose) in spring (Nelson 1964). Fresh scars were most often found in clusters of five or more closely grouped trees, all or most with their scars facing upslope. The upslope orientation and spring wounding (Kozlowski 1971) may be due to easier bark removal, but the thin bark of Alaska yellow-cedar (Anderson 1959) provides little protection against these powerful animals. We found groups of cedars with fresh scars every spring in May and June for seven consecutive years, suggesting that basal scarring occurs in these stands every year.

TABLE 1. Fungi collected (C) or isolated (I) from basal scars on Alaska yellow-cedar. Six classes of scar condition are based on wood deterioration.

Fungal species	Scar condition					
	1 fresh to 1 year old	2 sapwood sound, unstained	3 sapwood stained but firm	4 sapwood soft, intact	5 sapwood decayed, partially missing	6 heartwood exposed
ASCOMYCETES						
Bertia moriformis (Tode: Fr.) de Notaris		C	C	C	C	
Ceratocystis sp.	C,I	C				
Dothidea sp.		C,I				
Herpotrichia sp.		C	C			
Stictis radiata L. Pers. subsp. *radiata*	C					
BASIDIOMYCETES						
Auricularia auricularis (Hooke.) Underw.				C		
Armillaria sp.			C,I	C	C	
Cyathus olla (Batsch) ex Pers.					C	
Dacrymyces deliquescens (Merazt) Duby.		C		C	C	
Galerina sp.				C	C	
Hyphodontia aspera (Fr.) J. Erikss.				C		
Lactarius deliciosus (Fr.) S.F. Gray					C	
Lycoperdon sp.					C	
Pistillaria sp.	C	C				
Polyporus elegans Bull.: Fr.		C,I	C			
Skeletocutis amorpha (Fr.) Kotl. et Pouz.			C	C		
Xeromphalina campanella (Batsch: Fr.) Kuhn. & Maire.					C	
FUNGI IMPERFECTI						
Leptographium sp.	I	C,I				
Mycelium radicis atrovirens Melin		I				
Phialophora sp.		I				
Seiridium cardinale (Wagener) Sutton & Gibson		I				
Sporidesmium sp.	I	I				

The heights of fresh scars with bite marks corresponded closely with the modal height of all measured scars (fresh and old) (Figure 2). Some Alaska yellow-cedars had been repeatedly scarred, a dozen or more times around the base of their boles, showing a range of scar ages. These multi-scarred trees were most often adjacent to well-established bear trails. Brown bears are the only animals on these islands capable of such tree damage (J. Schoen, AK Dep. Fish and Game, pers. comm.). Their hair, scat, trails, and our sightings are evidence of their common occurrence in areas where Alaska yellow-cedars are scarred.

In southeast Alaska significant brown bear populations are restricted to Admiralty, Baranof, and Chichagof Islands and the mainland, with the greatest densities on the three islands (Meehan 1974, Alaska Department of Fish and Game 1977). Most other islands are inhabited by black bears (*Ursus americanus*) but not brown bears. Both bear species occur on the mainland. On Prince of Wales and Wrangell Islands, which have black but not brown bears (the latter are occasionally reported on Wrangell Island), we encountered no scars that resembled the shape of the scars described above. In our general observations throughout southeast Alaska, we have not observed scars on Alaska yellow-cedar in areas without large brown bear populations. Thus, basal scars on Alaska yellow-cedar were infrequent or absent in the absence of brown bears; however, scars were not necessarily frequent wherever Alaska yellow-cedar and brown bears coexist. Scars were infrequent at Kennel Creek, on Chichagof Island, where brown bears are common.

Basal scars are not the primary cause of Alaska yellow-cedar mortality in southeast Alaska. Scar incidence was not greater on dying cedar trees than on healthy trees, nor was it greater on cedars in declining than non-declining stands. Numerous Alaska yellow-cedar trees die with no basal scars (Shaw *et al.* 1985, Hennon *et al.* 1984). Basal scarring was most common in the well-drained, high volume forest type where mortality was least common (Hennon *et al.* 1984). Extensive mortality of Alaska yellow-cedar occurs on Prince of Wales, Wrangell, and other islands (USDA Forest Service 1988) where brown bears are absent and basal scarring was not found. A fresh wound on a declining, weakened Alaska yellow-cedar could, however, contribute to its death. In only a few cases did we observe trees that were completely girdled and died from basal scarring.

Bear damage to conifers has been reported frequently, but only once noted on Alaska yellow-cedar (Ruth and Harris 1979). Girdling of young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) by black bears is a serious problem in portions of western Washington and Oregon (Lawrence *et al.* 1961) where more than 50 percent of trees may be injured by black bears (Levin 1954). On the Kenai Peninsula in Alaska, scars interpreted to have been caused by black bears were common on white spruce (*Picea glauca* (Moench) Voss) and quaking aspen (*Populus tremuloides* Michx.) (Lutz 1951). The exposed wood in scars caused by black bears usually has shallow grooves made with teeth of lower jaws or claws (Lawrence *et al.* 1961). Such scars can occur from the tree base to 15 m or more up the bole (Childs and Worthington 1955). These vertical feeding marks are in sharp contrast to the horizontal bite marks that we found on Alaska yellow-cedars.

The 11 scars with horizontal cuts on Alaska yellow-cedar trees were likely caused by Alaska Natives collecting bark for making hats, baskets, clothing (Frear 1982), and roofs. Human-caused scars have been reported previously on Alaska yellow-cedar and western redcedar (*Thuja plicata* Donn ex D. Don) (USDA Forest Service 1982, Hicks 1984, Stewart 1984). All but one of the scars that we found was less than 100 m from the closest beach, where these large pieces of bark could have been easily gathered and transported.

Human-caused scars were not common, and this impact will probably be less consequential in the future even though some Alaska Native people still collect and use cedar bark. No recently caused human scars were found in the study areas, however. One of the 11 scars in Peril Strait was made 102 years ago. Similar scars were found in Prince William Sound, Alaska, and were dated to 180 years ago (C. G. Shaw III, unpublished data). The major impact of human-caused scars is that they occur on the largest Alaska yellow-cedar trees and, because of the scar size and age, are probably associated with internal wood decay found in these trees.

Tree responses to scarring and the decay resistance of the non-responsive heartwood seem to slow the radial advance of fungi and, thereby, retard decay. The bright yellow color present in surviving sapwood is probably a reaction to wounding and likely slows fungal advancement. Wood decay towards the pith in heartwood behind the scar is probably limited by the heartwood's anti-fungal compounds (Rennerfelt and Nacht 1955). A significant decay arc can develop vertically above the scar, however. The concept of tree responses to wounding is not new and has been described for many other tree species (Hepting and Blaisdell 1936, Shigo and Marx 1977).

Basal scars cause significant defect and may reduce the value of the butt log of scarred Alaska yellow-cedars to cull. Wood adjacent to scars may be salvageable unless the scar is very old, in which case decay fungi are less limited by tree responses and heartwood properties and decompose much of the bole's wood. Additional study is needed to quantify volume losses on trees with basal scars and to determine which fungi are most responsible for causing the vertical decay column. Several of the dark colored fungi we isolated from basal scars (e.g., *Phialophora, Sporidesmium,* and *Mycelium radicis atrovirens*) may be the same fungi that stain the heartwood of Alaska yellow-cedar (Smith 1970).

The common scarring of Alaska yellow-cedar trees on the better drained, productive sites may affect revenues from future timber sales in these areas. These sites have the tallest trees, the most total volume, and the highest proportion of spruce and western hemlock (Hennon *et al.* 1984). Thus, these stands are among the most likely to be harvested. A high degree of defect or cull of Alaska yellow-cedar, the most valuable wood in these stands, should be expected in stands where basal scarring is common.

In conclusion, we believe brown bears and, to a much lesser extent, humans are responsible for the numerous basal scars on Alaska yellow-cedar on Chichagof and Baranof Islands. These basal scars were not consistently associated with dying Alaska yellow-cedars and are not the primary cause of the extensive decline and mortality of this species.

Acknowledgments

Dr. John Schoen and LaVern Beier, both of the Alaska Department of Fish and Game, are gratefully acknowledged for their assistance in interpreting how brown bears scar cedars. Michael McWilliams, Marybetts Sinclair, Susan Hennon, and Mark Nay are sincerely thanked for their field assistance. We also greatly appreciate the use of the cabin at Poison Cove, made available by Irene Jimmy, during the course of these studies. This study was funded by USDA Forest Service Cooperative Agreement No. PNW-82-311.

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Received 27 March 1989
Accepted for publication 31 August 1989

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Limnology, Vegetation, and Classification of Coast Range Slump-formed Ponds

Abstract

Slump-formed ponds afford scarce riparian and aquatic habitats in north coastal California. This study provides information and a classification system for their management. Fourteen slump-formed ponds were studied in the Coast Range of northwestern California during 1975-1976 for limnological and vegetation characteristics. The ponds averaged 2.4 m maximum depth and 0.56 ha surface area. Subsurface contours and hypsographic curves suggested various stages of basin fill-in. Water quality (dissolved oxygen and temperature) and the presence of algae species (Nygaard's trophic index) provided evidence that the ponds were typically mesotrophic to eutrophic. Algal, submergent, emergent, and riparian vascular plant species were identified. Ponds were classified based on water permanence (ephemeral, astatic, and stable) and successional stage (degree of basin fill-in). Pond classes corresponded to unique combinations of limnological and vegetation characteristics. The pond classification system is useful for guiding management activities to rehabilitate, maintain, and enhance riparian and aquatic habitats associated with the ponds.

Introduction

Little is known of the physical and biological characteristics of slump-formed ponds in the Coast Range of the Pacific states, although the total area of wetland and fresh-water aquatic habitats is relatively small and has been declining in recent years in the west (e.g., Sands and Howe 1977). Specifically, the riparian habitat in the coastal foothills of Humboldt County in the Coast Range of northern California comprises 0.2 percent of the county's total acreage, but is the most valuable habitat as a concentration point for many floral and faunal species (California Department of Fish and Game 1965, Thomas *et al.* 1979).

This study was prompted by the need for understanding the limnological and vegetational characteristics of Coast Range slump-formed ponds as a basis for developing management criteria. The objectives of the study were to (1) describe physical and chemical limnological characteristics, (2) describe aquatic and riparian vegetation, and (3) develop a classification system, based on limnological and vegetation characteristics, for describing and predicting both physical and biological attributes.

Study Area

During 1975-1976, 17 ponds were located and studied on Six Rivers National Forest in the Coast Range of northwestern California. The ponds were identified from aerial photos (scale 1:15,840) and from field surveys and were chosen to represent a cross-section of physical and biological conditions. The steep slopes on which the ponds were found were typically composed of unstable regolith and mass-wasting was fairly common throughout the region.

The general study area is characterized by warm dry summers and cool wet winters. Average annual rainfall is 64-165 cm; average monthly precipitation is as high as 25-40 cm during November to January, and as low as 0-2 cm during July and August (data from Lower Trinity Ranger District office, Six Rivers National Forest, Willow Creek, California). Mean minimum monthly temperatures range 0-4°C during winter and 7-11°C during summer, and maximum temperatures range from 7-13°C during winter and 30-35°C during summer. Summer weather during the study was drier and warmer than average.

All ponds were within the Mixed Evergreen Forest with Chinquapin (*Castanopsis chrysophylla*) or Rhododendron (*Rhododendron macrophyllum*) vegetation types (Küchler 1977). Dominant tree species in these types are Douglas-fir (*Pseudotsuga menziesii*), tanoak (*Lithocarpus densiflora*) and Pacific madrone (*Arbutus menziesii*).

Methods

Limnological Surveys. Pond maximum length (l), breadth, surface area (A), and shoreline length (L) were measured on all ponds with a planimeter on aerial photos or on surface maps developed

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in the field by using an alidade and plane table (Welch 1948, Lind 1974). Mean breadth (A/1) and shoreline development indices ($L/2 \cdot \sqrt{[\pi A]}$) were calculated for each pond. The shoreline development index describes shape of each pond by comparing the shoreline length to a circle with the same area as the pond. The smallest possible value is 1.0, representing a circle, and index values increase as the shape becomes more irregular (Cole 1975, Lind 1974).

Maximum depth and percent relative depth of all ponds were measured by soundings from a raft. Hypsographic curves were estimated from benthic contours drawn for four ponds representing early and late stages of basin fill-in (Bee, Red Mountain, Onion, and Broken Rib Lakes). Calculations of morphologic parameters followed Cole (1975) and Welch (1948). Poles marked in 0.2 m intervals were placed in each pond and water permanence was measured by recording changes in surface elevations biweekly during 1975 and 1976 summers and bimonthly during the 1975-1976 year. Sediment depth was probed in all ponds during summer 1975 with a telescopic pole.

Temperature and dissolved oxygen (DO) were monitored at 0.3 m intervals with a portable DO and temperature meter (Model 1010 Delta Scientific Corporation) four times during late summer 1957 in four ponds representing variable or stable water conditions. The meter was calibrated immediately before each measurement. Five water samples were taken at random depths and locations from each pond and analyzed in the Six Rivers National Forest laboratory for pH, conductivity, and turbidity (Model 7 pH Meter, Corning Scientific Instruments; Model RB3 Conductivity Meter, Bechman Instruments; Model 2100A Turbidimeter, Hach Scientific Equipment).

Vegetation Sampling. Algae were sampled during summer at four ponds (Primal Pond, Bushwack Pond, Sucker Lake, and Big Lake) chosen because they varied greatly in physical characteristics (especially water permanence) and would provide a wide variety of species. The ponds sampled represented the wide range of ponds (except for the early successional ephemeral class) included in the classification system that was ultimately developed. Three algae samples were taken from each pond by plankton net tow, squeezings from submergent flora (tychoplankton), and skimming the water surface. Algae were identified to species and trophic state of each pond was indexed by the relative proportions of various species in the samples (Nygaard 1949).

Submergents, emergents, and riparian vegetation were sampled during summer at six ponds (Underwood, Bushwack, Primal, Greater Twin, Lesser Twin, and Duckweed Ponds) chosen to represent a spectrum of depth, surface area, degree of basin fill-in, and water permanence.

Submergent vegetation was sampled in each of the six ponds with 80 scoops of a rake at even intervals along two transects across each pond. Frequency of each species was determined (no. scoops a species was observed in/80 total scoops) and a descriptive scale for frequency of submergents was used (available from author). For purposes of this study, duckweeds were considered as submergents because they occurred in the scoop samples. Density (no. stems/m^2) of each stand of emergent vegetation was estimated by averaging the number of stems within a wire frame (1 x 1 m) placed randomly at 20 locations within each emergent stand.

Riparian vegetation was sampled by use of fixed-area plots, the size of which was determined from species-area curves derived from nested quadrats (Dosting 1958). Plot shapes were rectangular (sides 3:1, the longer running parallel to the shoreline). Twenty plots were distributed evenly around each shoreline and vegetation was assessed by using the Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). Percent frequency was calculated and modal cover determined of species over 10 percent frequent.

Quantitative descriptions of submergent, emergent, and shoreline vegetation from the six ponds were supplemented by qualitative observations of pond basins and vegetation made at all 17 ponds. Descriptions included pond basin topography, and frequency and cover of vegetation species estimated by eye.

Pond Classification. The purpose of developing a classification system was to identify unique structural and floristic attributes of different types of ponds to help predict physical and biological responses to management activities and guide management strategies. Classification based on vegetation characteristics alone was not sufficient for this purpose. The intent was to

devise a system by which vegetation characteristics could be predicted from other, physical attributes of the ponds.

To devise the classification system, results of the vegetation samples and qualitative descriptions of all ponds were related to the chemical, physical, and trophic attributes of the ponds. Since most ponds were mesotrophic to eutrophic, trophic state was not a helpful criterion to distinguish among ponds. Water quality (pH, conductivity, turbidity, dissolved oxygen content) seemed to vary in response to physical conditions of the pond basins and associated vegetation.

Ultimately, the ponds were classified based on water permanence and successional stage (Table 1). Following Cole (1975), successional stage was defined as degree of basin fill-in. Successional stage was described qualitatively as "early" if the pond basin was relatively steep and had only a shallow muck depth, and "late" if the pond basin was gently sloped and had a deep amount of muck and sediment. In this classification, degree of basin fill-in did not necessarily correlate with trophic condition. Water permanence classes included stable, astatic, and ephemeral ponds. Also, successional stages (early and late stages) of ephemeral ponds correlated with diagnostic characteristics. Limnological and vegetation characteristics were related to each of the pond classes.

Results and Discussion

Limnology

The ponds were likely formed by the mass-wasting process of soil creep, a slumpage that created small basins that filled with snow-melt, seep springs, or runoff. On average, the ponds measured 133 m maximum length, 71 m maximum breadth, and 38 m average breadth (Table 2). Surface area averaged 0.56 ha and shoreline length averaged 328 m. Most ponds were roughly oval in shape (average shoreline development index of 1.33).

Water permanence varied among the ponds, although maximum depth averaged only 2.4 m. Seven ponds were relatively stable over the summer, varying less than 10 percent from their maximum depth. Four ponds were more astatic and varied in surface elevation over the year by as much as 55 percent from their maximum depth. For example, Sucker Lake varied 2.5-5.6 m

TABLE 1. Classification characteristics of Coast Range slump-formed ponds.

	Slump pond class			
			Ephemeral	
Feature	Stable	Astatic	Early successional	Late successional
Surface elevation variation	<10% from max. depth; never dries	>10% from max. depth; dries infrequently	dries regularly	
Emergent stands	discrete, dense	little or none	none	dispersed
Floating mats	peripheral	few or none	none	central
Shoreline evaporation zone	narrow, little "feather edge," with shrubs	broad; with annuals, lush sedge and/or mud recently flooded or exposed	very narrow or absent	narrow to broad, with exposed mud
Substrate	deep, soft muck	moderately deep mud and peat	steep; mud or gravel	shallow; gently sloped or level; deep mud
Floating logs	typically many, with lush veg. growth	several; sparse to mod. veg. growth	few; no veg. growth	several; sparse to mod. veg. growth
Inflow	perennial; spring-fed	perennial or seasonal; spring- or runoff-fed	seasonal; runoff-fed	

TABLE 2. Physical limnological characteristics of Coast Range slump-formed ponds.

Pond	Surface measures						Subsurface measures		Pond class[a]
	Maximum length (m)	Breadth (m)	Mean breadth (m)	Surface area (ha)	Shoreline length (m)	Shoreline development index	Maximum depth (m)	Percent mean slope	
Broken Rib L.	81	30	15	0.12	189	1.51	3.5	18	Early Stable
Blue L.	175	75	54	0.94	474	1.37	5.6	1	Early Stable
Bee L.	279	152	27	0.74	369	1.21	1.8	4	Late Stable
Red Mt. L.	213	68	37	0.78	503	1.60	2.0	4	Late Stable
Onion L.	124	71	47	0.59	318	1.17	2.0	5	Late Stable
Primal Pond	101	64	39	0.39	337	1.52	5.0	14	Late Stable
Bushwack Pond	113	50	31	0.35	280	1.34	2.4	7	Late Stable
Sucker L.	176	50	23	0.41	402	1.77	2.5	7	Early Astatic
Duckweed Pond	84	64	43	0.36	213	1.00	1.5	4	Late Astatic
Underwood Pond	56	39	27	0.15	156	1.14	3.0	14	Late Astatic
Greater Twin P.	70	48	40	0.28	195	1.04	1.1	4	Late Astatic
Hidden Pond	70	40	nd[b]	nd	250	nd	4.0	nd	Early Ephemeral
Lesser Twin Pond	66	39	29	0.19	175	1.14	1.8	7	Early Ephemeral
Big L.	251	201	81	2.04	731	1.45	1.5	2	Late Ephemeral
MEANS	133	71	38	0.56	328	1.33	2.4[c]	7	

[a]Successional stage (early, late) or degree of basin fill-in and degree of water permanence (stable, astatic, ephemeral). See text for descriptions.
[b]nd = no data.
[c]Based on 17 ponds (three additional ponds measured 0.8, 1.1, and 1.1 m maximum depth).

maximum depth from summer to winter. One pond (Hidden Pond, Table 2) measured 4.0 m maximum depth during spring but dried in a period of 24 days (17 June to 10 July). Water permanence varied probably because of differences in water sources and permeability of substrates. Because of the shallowness, all ponds studied are probably polymictic, i.e., characterized by many or continual overturn periods (Cole 1975).

The percent hypsographic curves of the three late successional, stable ponds (Bee, Red Mountain, and Onion Lakes) were concave in form (Figure 1). This shape represented gently sloping shorelines and broad, shallow, flat bottoms, characteristic of ponds in late stages of basin fill-in. The curve of the early successional, stable pond (Broken Rib Lake) was more convex in shape, representing steeper basin walls and a more angular bottom. Over all ponds, basin slope was moderately gentle; relative slope of the bottom averaged 7 percent (Table 2). Basin shapes were likely a result of (1) topographic contours of the slump concavity and (2) degree of siltation

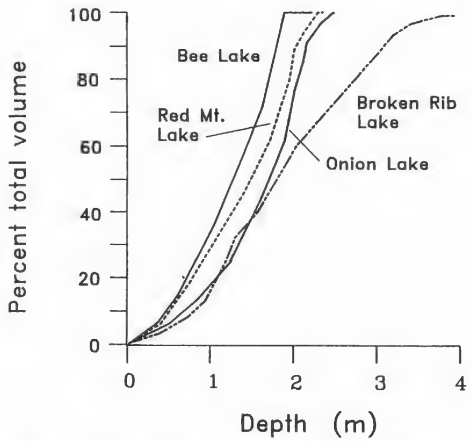

Figure 1. Percent volume hypsographic curves of four stable, slump-formed ponds in the north Coast Range of California. Broken Rib Lake is in an early successional stage of basin fill-in; the others are in late stages.

or fill-in (successional stage). In general, the ponds that were in a later stage of fill-in (e.g.,

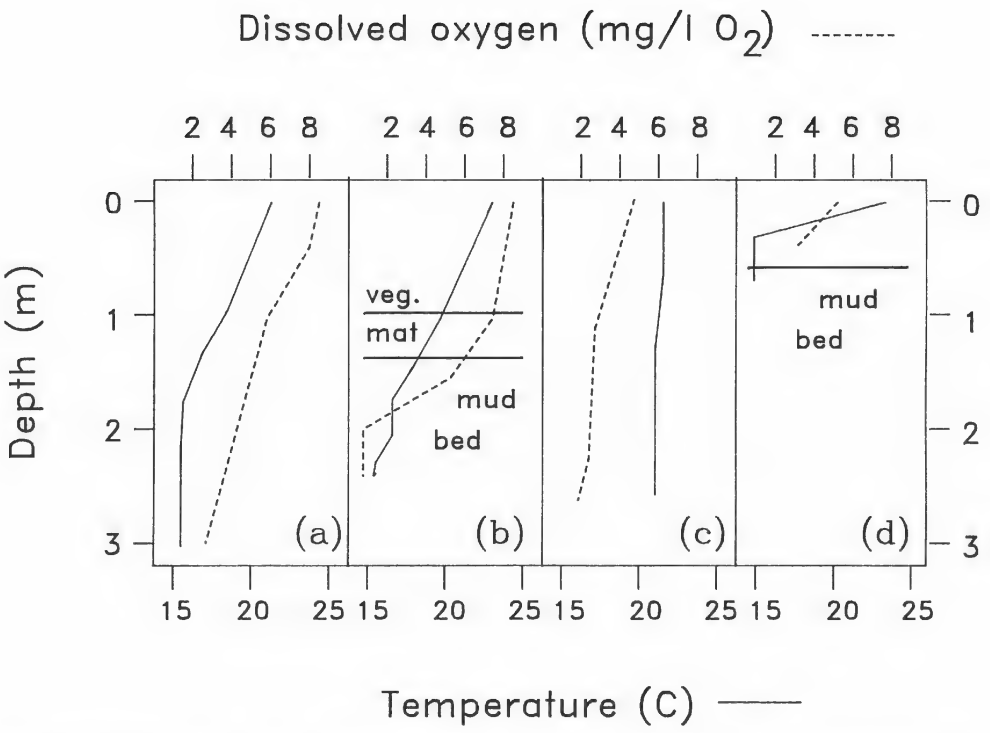

Figure 2. Temperature (T) and dissolved oxygen (DO) profiles of pond classes during summer. (a) Late-successional stable pond (29 June, Primal Pond [see Table 2 for other pond characteristics]). (b) Late successional stable pond with subsurface mat of *Myriophyllum exalbescens* ssp. *exalbescens* (22 July, Bushwack Pond). (c) Early successional astatic pond (5 August, Sucker Lake). (d) Late-successional ephemeral pond (24 August, Big Lake).

Big Lake, Greater Twin Pond and Duckweed Pond, Table 2) were shallower (lower maximum depth), more gently sloped (lower percent mean slope), and had greater sediment depths than ponds in an earlier stage (e.g., Primal Pond, Broken Rib Lake). Late successional ponds accumulated sediments of up to 1.8 m depth, whereas early successional ponds had sediment depths of 0-0.5 m.

Temperature and DO profiles (Figure 2) revealed marked differences among the four ponds sampled, owing to various maximum depths, vegetation composition, and basin shapes. None of the ponds that were measured exhibited thermal stratification. DO levels varied from 8 mg/l at the surface to less than 2 mg/l at the bottom. DO curves typically exhibited an orthograde profile (Figures 2a, 2c), characterizing an even oxygen distribution during overturn (Cole 1975).

Both temperature and DO curves in one pond (Bushwack Pond; Figure 2b) resulted from the presence of a sub-surface vegetation mat of water milfoil (*Myriophyllum spicatum* ssp. *exalbescens*) and an underlying organic matter bed. The DO curve exhibited a clinograde profile, characterizing a stratified eutrophic lake with a large vegetation biomass in the epilimnion and a stagnant hypolimnion (Cole 1975). However, the near-linear temperature curve and shallow maximum depth (2.4 m) suggested that thermal stratification was unlikely.

Temperature and DO curves in one pond (Sucker Lake) that lacked emergent rooted vegetation were nearly vertical (Figure 2c). This was probably because of the lake's shallow depth (2.5 m) and openness to variable winds (located on a ridge) and thus continual overturn. DO levels were quite low. The temperature curve was nearly

isothermal, with a surface-bottom gradient of only 1.2°C.

The temperature profile in one shallow ephemeral pond (Big Lake) was quite steep (Figure 2d). The presence of a thick mat of yellow pond-lily (*Nuphar polysepalum*) extending from the surface to the maximum testable depth of 0.6 m was the probable cause of a temperature gradient of 11.5°C over that depth.

The pH varied from neutral to slightly basic (mean 7.1, range 7.0 to 7.4). Conductivity values ranged 130-500 (mean 274) micromhos/cm. Turbidity values ranged widely among the ponds, 68-560 JTUs (mean 217) (Table 3).

TABLE 3. Water quality characteristics of four Coast Range slump-formed ponds. Five water samples were taken from each pond during August and September 1975.

Pond	pH	Conductivity (micromhos/cm)	Turbidity (JTU's)
Primal Pond			
range:	6.95-7.05	370-500	68-110
mean:	7.00	406	86
Bushwack Pond			
range:	6.95-7.15	230-260	71-140
mean:	7.06	250	87
Sucker Lake			
range:	7.20-7.30	260-300	230-420
mean:	7.24	290	284
Big Lake			
range:	7.05-7.35	130-180	240-560
mean:	7.17	149	410

Vegetation

Algae species. Although the ponds were sampled during summer—a season which exhibits the greatest number of eutrophic indicators (e.g., blue-greens and Chlorococcales)—and pulses of different algae groups only a few days apart could greatly alter the indices, some generalizations can be made.

All four ponds sampled exhibited a well-rounded series of algal communities (list of algae species is available from the author upon request). A total 105 species were directly identified or inferred. The total number of species in any one pond ranged as high as 25 from the plankton tow samples, 36 from the tychoplankton samples, 25 from the surface skim samples, and 59 from all samples combined.

Samples were taken during late summer, accounting for the high number of taxa (27) of blue-green algae present. The presence of *Aphanizomenon flosaquae* and *Microcystis aeruginosa* in the samples at low levels of abundance indicated fairly healthy environments. Monitoring these eutrophic indicators as well as the desmids and flagellates over the year could reveal much about the annual trophic health of each pond and degree of input of organic material from the local watershed. The abundance of *Mougeotia* and *Spirogyra,* and populations of epiphytic and tychoplanktonic diatoms which accompany them, also indicated healthy environments with a moderate diversity denoting mesotrophy or early eutrophy. Values of Nygaard's Trophic Index (Nygaard 1949) also suggested mesotrophic to eutrophic conditions (Table 4).

TABLE 4. Trophic state of Coast Range slump-formed ponds (results of applying Nygaard's Trophic Index [Nygaard 1949]). All ponds were sampled on 1 September 1975.

	Indices[a]				
Pond	MYX	CHL	DIA	EUG	COM
Primal Pond	2.5—E	0.5—E	0.1—M	0.2—M	4.0—E
Bushwack Pond	1.0—E	3.0—E	0/5—M	0.1—M	4.5—E
Sucker Lake	3.0—E	5.0—E	0/10—M	0/8—M	8.0—E
Big Lake	0/1—M	0/1—M	0/6—M	0/0—M	0/1—M

[a]MYX = Myxophycean = Myxophyceae/Desmideae
CHL = Chlorophycean = Chlorococcales/Desmideae
DIA = Diatom = Centrales/Pennales
EUG = Euglenine = Euglineae/(Myxophyceae + Chlorococcales)
COM = Compound = (Myxophyceae + Chlorococcales + Centrales + Euglenineae)/Desmideae
M = mesotrophic
E = eutrophic

The presence of *Eremoshaera viridis* in Primal Pond may be a new record for the western U.S. This range extension is previously undocumented. Also, it was noticeably smaller in size than those found in eastern U.S. and Europe.

Submergents. A total of nine submergent vascular species and two submergent rooted

algae (*Chara* spp.) were identified (list of species and vegetation associations is available from the author upon request). Submergent vegetation richness varied from 3 to 7 species in any one pond. Frequency and dominance varied among submergent species within and among ponds. The pondweed *Potamogeton natans,* found in all ponds surveyed for vegetation, was never dominant in frequency or density. The dominant submergents were star duckweed (*Lemna trisulca*), lesser duckweed (*L. minor*), stonewort, and water milfoil. Other submergents occurred as subdominants and at lower frequencies and densities. Buttercup (*Ranunculus aquatilis*) was observed only in ponds that varied at least 10 percent from maximum depth over a year's time.

One species of bulrush (*Scirpus subterminalis*) was observed in a stable pond. The species was growing erect as a submergent in up to 0.3 m water and as an emergent in as little as 6 cm water. This is the first specimen from the Coast Range of California (herbaria searched: UC, HSC, CAS, JEPS).

Emergents. Four emergent macrophytes were recorded. The richest emergent flora at any one pond consisted of three species. Densities of emergent stands varied among the ponds. Yellow pond-lily was as dense as 20-50 stems/m^2 and soft-stemmed bulrush (*Scirpus validus*) was as dense as 50-300 stems/m^2. Dominance of emergents also varied considerably. Ponds in advanced stages of fill-in typically had lush stands of pond-lily, bulrush, or broad-leafed cattail (*Typha latifolia*); these stands were widely dispersed across surfaces of ponds that varied considerably in surface elevation, and were in discrete stands in the more stable ponds.

Also creating an interspersion with open water in stable ponds were floating logs with lush vegetational growth of grasses, sedges (*Carex* spp.), and sundry herbs. Among all species of macrophytes, cinquefoil (*Potentilla* sp.) was observed only in stable ponds, whereas foxtail (*Alopecurus* sp.) was observed only in ephemeral ponds.

Shoreline evaporation zone. Shoreline riparian vegetation showed high variation among ponds. Riparian vegetation was floristically rich. The dominant shrubs were nine-bark (*Physocarpus capitatus*), willow (*Salix sitchensis* and *S. lasiandra* var. *lancifolia*), red alder (*Alnus rubra*), and poison oak (*Toxicodendron diversiloba*). The dominant herbs were water hemlock (*Cicuta douglasii*), mint (*Mentha arvensis*), and sedge (*Carex exsiccata*). Sedge often formed lush shoreline belts around ponds that varied seasonally in water level more than 10 percent of maximum depth. Other shrubs and herbs occurred as subdominants in the shoreline zone. Panic grass (*Panicum capilare*) was found only at ephemeral ponds which typically lacked riparian shrubs. Several riparian species were found only at stable ponds: cinquefoil, sedge (*Carex hindsii*), sundew (*Drosera rotundifolia*), water hemlock, poison oak, and berry (*Rubus ursinus*).

One riparian species (*Dulichium arundinaceum*) was found in a late-successional pond (Big Lake) on a muddy floating mat. This species is rare in California (Mason 1969, Munz 1968). Only two previous specimens from Humboldt County and 10 specimens in other California counties were discovered in four herbaria searched (UC, HSC, CAS, JEPS). (Voucher specimens of *Scirpus subterminalis* and *Dulichium arundinaceum* are deposited at Humboldt State University, Arcata, California herbarium.)

Classification

Ponds were classified based on degree of water permanence and degree of basin fill-in, as follows (Table 1).

Stable ponds. Surface level varied approximately 10 percent or less from maximum depth. Stable ponds can be recognized by discrete stands of bulrush, cattail, and other emergents; peripheral floating mats; an interspersion of open water and submergent vegetation; a substrate of deep, soft muck; a narrow shoreline evaporation zone with little "feather edge" exposed mud; lush vegetational growth on numerous floating logs; and by being perennially spring-fed.

Astatic ponds. Surface level varied more than 10 percent from maximum depth; the ponds dried infrequently. Astatic ponds can be recognized by little or no perennial emergent vegetation; few or no floating mats; a recently flooded or exposed shoreline belt of vegetation; a substrate of moderately deep mud and peat; a broad shoreline evaporation zone with annual species, lush sedge, and/or exposed mud; floating logs being less numerous than in stable ponds and with sparse to moderate vegetational growth; and by

being fed perennially or seasonally by springs or runoff.

Ephemeral ponds. These ponds dry regularly. Those in an early successional stage can be recognized by the absence of emergent vegetation; no floating mats; a very narrow or absent shoreline evaporation zone; a steeply-walled substrate of mud or gravel; few floating logs with no vegetational growth; and by usually being fed seasonally by runoff. Ephemeral ponds in a late successional stage can be recognized by emergent vegetation occurring in more or less dispersed stands; central floating mats; a narrow to broad shoreline evaporation zone and exposed mud areas; a shallow and gently sloped or level bottom of deep mud; floating logs being less numerous than in stable ponds and with sparse to moderate vegetational growth; and by usually being fed seasonally by runoff.

Indicator plant species were identified for each pond class by growth form (submergent, emergent, and shoreline riparian) (Table 5). The recognition of pond classes in the field, based on physiognomic and floristic features, may aid in formulating management plans. For example, if a pond has characteristics of an ephemeral system, objectives for habitat management or use of the pond as a water source may differ than if the characteristics suggest a stable system. Natural draw-downs of unstable ponds are probably beneficial for seeding desirable food or cover plant species for wildlife, for consolidating oozy bottoms for a better substrate to support rooted vegetation, for exposing an aquatic prey base for wildlife predators, and for encouraging beneficial changes of water and soil chemistry (Marcot 1978).

Acknowledgments

This study was conducted under contract No. 10-472-77 with USDA Forest Service, Six Rivers National Forest. I am grateful to the following personnel for their assistance: N. Brown, M. Delamore, R. Hill, J. Kahl, B. Klipfel, D. LaVen, G. Liesten, S. Loe, D. Osmundson, E. Payne, and D. Solis. I am grateful also to J. Hilgert of the Environmental Protection Agency for his identification and discussion of algae distributions. Comments from K. V. Kardong and three anonymous reviewers improved the manuscript.

TABLE 5. Indicator plant species identified for pond classes (see Table 1 for descriptions of pond classes).

	Pond Class		
	Stable	Astatic	Ephemeral
Submergents	(no indicators)	*Ranunculus aquatilus*[a]	*Ranunculus aquatilus*[a]
Emergent	*Potentilla* sp.	(no indicators)	*Alopecurus* sp.
Shoreline zone	*Potentilla* sp. *Carex hindsii* *Drosera rotundifolia* *Cicuta douglasii* *Toxicodendron diversiloba* *Rubus ursinus* In general, forest influence in the thin shoreline zone.	*Mentha arvensis*[a] *Rorippa curvisiliqua*[a] *Carex athrostachya*[a] *Trichostema laxum*[a] In general, dry site species in the receding shoreline zone.	*Alopecurus* sp. *Panicum capilare* *Mentha arvensis*[a] *Rorippa curvisiliqua*[a] *Carex athrostachya*[a] *Euphorbia serpyllifolia*[b] *Trichostema laxum*[ab]

[a]Indicator species for either astatic or ephemeral ponds.
[b]Indicator species for early-successional ephemeral ponds.

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Received 27 April 1989
Accepted for publication 8 September 1989

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Northwest Science
Volume 63 (1989)
Author and Subject Index

[All author entry headings are in capital letters. Abstract numbers are shown in parentheses (abs. #) after page numbers.]

AIDS epidemic
  model for spread and control: Palmer and Moody, 68 (abs. 26)
Abies *see* firs
Alaska
  spruce beetles: Hard, 5-12
  understory biomass: Yarie and Mead, 221-231
alder, red (*Alnus rubra*)
  leaf water potential: Lu and Zaerr, 68 (abs. 25)
  seedling growth: Giordano and Hibbs, 66 (abs. 20)
ALLEN, B.H. and J.W. BARTOLOME. Cattle grazing effects on understory cover and tree growth in mixed conifer clearcuts. 214-220
Alnus *see* alder
ANTHONY, R.G. *see* DellaSala *et al.,* 104-108
Aplodontia *see* mountain beaver
Artemisia *see* sagebrush
Ascaphus *see* frogs, tailed
ATKINSON, K. *see* Milne *et al.,* 83-86

BARNHURST, D. and F.G. LINDZEY. Detecting female mountain lions with kittens. 35-37
BARTOLOME, J.W. *see* Allen and Bartolome, 214-220
bats
  in southern Idaho: Wackenhut and Keller, 65 (abs. 14)
bears, black (*Ursus americanus*)
  food habits: MacHutchon, 116-118
beaver (*Castor canadensis*)
  and Oregon streams: Leidholt *et al.,* 71 (abs. 37)
BECHARD, M.J. *see* McAnnis and Bechard, 64 (abs. 12)
BECHARD, M.J. *see* Spahr and Bechard, 65 (abs. 13)
beetles, spruce (*Dendroctonus rufipennis*)
  in spruce stand: Hard, 5-12
BENHAM, S.R., F.L. TOBIASON and M.J. THEILMAN. Vivianite from Kalaloch, Olympic Penninsula, Washington. 73 (abs. 48)
BETTS, B.J. Range and habitat preferences of Washington ground squirrels. 66 (abs. 17)
BIDLAKE, W.R., G.S. CAMPBELL and R.I. PAPENDICK. Seed zone temperature and moisture conditions in a partially frozen soil/crop residue system. 69 (abs. 29)
biomass estimates
  of forest vegetation: Yarie and Mead, 221-231
birds
  bald eagles: Spahr and Bechard, 65 (abs. 13)
  Canada geese surveys: Krohn and Bizeau, 1-4
  Canada goose habitats: Passmore and Bittler, 64 (abs. 10)
  Canada goose nests: Eberhardt, 62 (abs. 3)
  in Columbia Basin: Fitzner, 63 (abs. 5)
  and dam construction: Monda and Reichel, 13-18
  ferruginous hawks: McAnnis and Bechard, 64 (abs. 12)
  Forster's tern reproduction: Hall, 90-95
  great gray owls: Bull *et al.,* 38-43
bitterbrush, antelope (*Purshia tridentata*)
  germination: Meyer, 146-153
BITTLER, C. *see* Passmore and Bittler, 64 (abs. 10)
BIZEAU, E.G. *see* Krohn and Bizeau, 1-4
BLACK, R.A. *see* Evans *et al.,* 66 (abs. 19)
BOE, L., C.J. CHRISTIANSON and M.F. PASSMORE. Canada goose production on Lake Wallula and the lower Snake River. 64 (abs. 11)
BOONE, J.D. and B.L. KELLER. Small mammal activity and edge use on the subsurface disposal area, Idaho National Engineering Laboratory site. 65 (abs. 16)
BRANDT, C.A. and W.H. RICKARD, Jr. Restoring the Washington shrub-steppe: the basalt waste isolation reclamation project. 64 (abs. 9)
Branta *see* geese
British Columbia
  Canada geese: Passmore and Bittler, 64 (abs. 10)
  cheatgrass introduction: Novak and Mack, 67 (abs. 21)
  wolves: Milne *et al.,* 71 (abs. 40)
Bromus *see* cheatgrass
BROWN, H. Thyroxine and induced metamorphosis in overwintering tadpoles of the tailed frog, *Ascaphus truei.* 72 (abs. 42)
BRYANT, L.D. *see* Filip *et al.,* 211-213
buckwheat, round-headed (*Eriogonum sphaerocephalum*)
  response to burning: Rickard, 144-145
BULL, E.L., M.G. HENJUM and R.S. ROHWEDER. Reproduction and mortality of great gray owls in Oregon. 38-43
BUTLER, D.R. Snow avalanche-dams and resultant hazards in Glacier National Park, Montana. 109-115

CAMAIONI, D.M. *see* Fryxell *et al.,* 73 (abs. 47)
CAMERON, K.A. Devils Kitchen thermal area at Mount Hood, Oregon, revisited. 73 (abs. 45)
CAMPBELL, C.L. *see* Carey *et al.,* 70 (abs. 36)
CAMPBELL, D.L. and J. EVANS. Aversive conditioning with thiram to reduce mountain beaver damage to Douglas-fir seedlings. 70 (abs. 35)
CAMPBELL, D.L. *see* Carey *et al.,* 70 (abs. 36)
CAMPBELL, G.S. *see* Bidlake *et al.,* 69 (abs. 29)
Canis *see* wolves
Cardaria *see* whitetop
CAREY, M.G., D.L. CAMPBELL and C.L. CAMPBELL. Physical structure, flora and fauna of mountain beaver nests. 70 (abs. 36)
CARSON, R.J. On impacts, volcanoes and extinctions. 129-131
CARTER, R.E. *see* Klinka *et al.,* 19-28
Cascade Range, Wa
  glaciation: Long, 96-103
Castor *see* beaver
cattle
  grazing and conifer seedling growth: Doescher *et al.,* 232-240
  grazing and shrubs and trees: Allen and Bartolome, 214-220
Centaurea *see* knapweed; starthistle
Cervus *see* elk
cheatgrass
  introduction pattern: Novak and Mack, 67 (abs. 21)
CHOW, M. *see* Fryxell *et al.,* 73 (abs. 47)
CHRISTIANSON, C.J. *see* Boe *et al.,* 64 (abs. 11)

Columbia basin and river, Wa
birds: Fitzner, 63 (abs. 5)
Canada geese: Eberhardt, 62 (abs. 3); Passmore and Britten, 64 (abs. 10)
cold desert spring-streams: Cushing, 62 (abs 1)
elk: McCorquodale, 62 (abs. 4); McCorquodale *et al.*, 29-34
fish resources: Dauble, 62 (abs. 2)
Forster's tern on islands: Hall, 90-95
plant distribution: Simmons *et al.*, 63 (abs. 6)
plant response to drought: Link *et al.*, 63 (abs. 7)
restoring shrub-steppe: Brandt and Rickard, 64 (abs. 9)
sagebrush steppe flora: Taylor, 63 (abs. 8)
conifers
seedling growth, water and cattle: Doescher *et al.*, 232-240
COX, G.W. Early summer diet and food preferences of northern pocket gophers in north central Oregon. 77-82
CRAWFORD, R.L. *see* Stevens and Crawford, 70 (abs. 34)
Crotalus *see* rattlesnakes
CUSHING, C.E. Structure and function of cold desert spring-streams. 62 (abs. 1)

dams
and avian community changes: Monda and Reichel, 13-18
caused by snow avalanches: Butler, 109-115
DAUBLE, D.D. Fishery resources of the Hanford Reach, Columbia River. 62 (abs. 2)
DELLASALA, D.A., C.L. THOMAS and R.G. ANTHONY. Use of domestic sheeep carrion by bald eagles wintering in the Willamette Valley, Oregon. 104-108
Dendroctonus *see* beetles
dinoseb
in soil: Stevens and Crawford, 70 (abs. 34)
DOESCHER, P.S., S.D. TESCH aand W.E. DREWIEN. Water relations and growth of conifer seedlings during three years of cattle grazing on a southwest Oregon plantation. 232-240
Douglas-firs (*Pseudotsuga menziesii*)
as Christmas trees: Hanley, 68 (abs. 27)
commercial thinning: Emmingham and Shainsky, 67 (abs. 24)
mountain beaver damage: Campbell and Evans, 70 (abs. 35)
and salal: Klinka *et al.*, 19-28
seedling growth: Radwan, 68 (abs. 28)
sheep production in plantations: Leininger *et al.*, 195-200
see also firs, noble
DOWNS, J.L. *see* Link *et al.*, 63 (abs. 7)
DREWIEN, W.E. *see* Doescher *et al.*, 232-240
drought
plant response: Link *et al.*, 63 (abs. 7)
Washington, 1986-88: Quinn, 72 (abs. 44)

eagles
in Columbia Basin: Fitzner, 63 (abs. 5)
bald (*Haliaeetus leucocephalus*)
and sheep carrion: DellaSala *et al.*, 104-108
wintering distribution: Spahr and Bechard, 65 (abs.13)
EBERHARDT, L.E. Nesting populations of Canada geese on the Hanford Reach, 1953-1988. 62 (abs. 3)
ecological process
and plant distribution: Simmons *et al.*, 63 (abs. 6)
elk (*Cervus elaphus*)
Hanford Site population: McCorquodale, 62 (abs. 4)
home ranges: McCorquodale *et al.*, 29-34
EMMINGHAM, W.H. and L.J. SHAINSKY. Comparison of high and low thinning of westside Douglas-fir: five year growth response. 67 (abs. 24)
Eriogonum *see* buckwheat
EVANS, J. *see* Campbell and Evans, 70 (abs. 35)
EVANS, R.D., R.A. BLACK and S.O. LINK. Carbon allocation to reproduction during drought in *Artemisia tridentata.* 66 (abs. 19)
EVANS, R.D. *see* Link *et al.*, 63 (abs. 7)
extinctions
impacts and volcanic theories: Carson, 129-131

Felis *see* mountain lions
FELLER, M.C. *see* Klinka *et al.*, 19-28
FILIP, G.M., L.D. BRYANT and C.A. PARKS. Mass movement of river ice causes severe tree wounds along the Grande Ronde River in northeastern Oregon. 211-213
fires
and buckwheat: Rickard, 144-145
Yellowstone area, in 1988: Schullery, 44-54
firs, noble (*Abies procera*)
as Christmas trees: Hanley, 68 (abs. 27)
see also Douglas-firs
fish
bull trout: Fraley and Shepard, 133-143
Hanford Reach, Columbia River: Dauble, 62 (abs. 2)
trout and stream gradients: Kozel *et al.*, 175-182
FITZNER, R.E. Seasonal diversity and abundance of hawks, owls and eagles in the Columbia Basin of southcentral Washington. 63 (abs. 5)
Flathead Lake and River system
migratory bull trout: Fraley and Shepard, 133-143
forestry
conifer seedlings and grazing: Doescher *et al.*, 232-240
Douglas-fir thinning: Emmingham and Shainsky, 67 (abs. 24)
fertilization of firs: Hanley, 68 (abs. 27)
forest floor and conifer growth: Radwan, 68 (abs. 28)
grazing and tree growth: Allen and Bartolome, 214-220
ice and tree wounds: Filip *et al.*, 211-213
mountain beaver control: Campbell and Evans, 70 (abs. 35)
Pinus halepensis in Jordan: Larsen and Higgins, 67 (abs. 23)
red cedar water use: Lu and Zaerr, 68 (abs. 25)
salal and tree growth: Klinka *et al.*, 19-28
and sheep production: Leininger *et al.*, 195-200
spruce beetle attacks: Hard, 5-12
tillage and pine seedlings: McNabb and Hobbs, 241-245
understory biomass determination: Yarie and Mead, 221-231
FRALEY, J.J. and B.B. SHEPARD. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. 133-143
frogs, tailed (*Ascaphus truei*)
metamorphosis: Brown, 72 (abs. 42)
FRYXELL, G.E., M. CHOW, W.A. RODIN and D.M. CAMAIONI. Electron transfer and radical cation reaction rates of methoxylated bibenzyls. 73 (abs. 47)

Garnet Hill, Nevada
rhyolite and tuffs: Hollabaugh *et al.*, 201-210
Gaultheria *see* salal
GEE, G.W. *see* Link *et al.*, 63 (abs. 7)

geese, Canada (*Branta canadensis*)
brooding habits: Passmore and Bittler, 64 (abs. 10)
nesting populations: Eberhardt, 62 (abs. 3)
production: Boe *et al.,* 64 (abs. 11)
tail fan surveys: Krohn and Bizeau, 1-4
geology
extinctions, volcanism and impacts: Carson, 129-131
Garnet Hill, Nevada: Hollabaugh *et al.,* 201-210
Leavenworth glaciation: Long, 73 (abs. 46); 96-103
Mount Hood thermal area: Cameron, 73 (abs. 45)
small mammal fauna from Touchet Beds: Spencer, 167-174
vivianite from Olympic Peninsula: Benham *et al.,* 73 (abs. 48)
GIORDANO, P. and D.E. HIBBS. Growth and carbon allocation of red alder seedlings grown over a density gradient. 66 (abs. 20)
glaciation
Leavenworth substage: Long, 96-103
Glacier National Park, Montana
snow avalanche-dams: Butler, 109-115
Grande Ronde River, Or
ice movement and tree damage: Filip *et al.,* 211-213
grass
and knapweeds: Larson and McInnis, 162-166
Grayia spinosa
and drought: Link *et al.,* 63 (abs. 7)

habitats
beaver and streams: Leidholt *et al.,* 71 (abs. 37)
and birds: Monda and Reichel, 13-18
Douglas-fir ecosystems: Klinka *et al.,* 19-28
and stream gradients: Kozel *et al.,* 175-182
restoring shrub-steppe: Brandt and Rickard, 64 (abs. 9)
Haliaeetus *see* eagles, bald
HALL, J.A. Aspects of Forster's tern (*Sterna forsteri*) reproduction cobblestone islands in southcentral Washington. 90-95
HALLET, J.G. *see* O'Connell and Hallet, 71 (abs. 38)
HALSE, R.R., B.A. ROTTINK and R. MISHAGA. Studies in *Sidalcea* taxonomy. 154-161
Hanford Site, Wa
wildlife: Rickard and Poole, 183-193
HANLEY, D.P. Fertilization and liming of Douglas-fir and noble fir Christmas trees. 68 (abs. 27)
HARD, J.S. Sequence of trees attacked by spruce beetles in a mature even-aged spruce stand in south-central Alaska. 5-12
HARESTAD, A.S. *see* Milne *et al.,* 83-86
hawks
in Columbia Basin: Fitzner, 63 (abs. 5)
home range: McAnnis and Bechard, 64 (abs. 12)
hemlock, western (*Tsuga heterophylla*)
seedling growth: Radwan, 68 (abs. 28)
HENJUM, M.G. *see* Bull *et al.,* 38-43
herbicides *see* dinoseb
herbivores
diet analysis: McInnis *et al.,* 71 (abs. 40)
HIBBS, D.E. *see* Giordano and Hibbs, 66 (abs. 20)
HIBBS, D.E. *see* Leidholt *et al.,* 71 (abs. 37)
HIGGINS, S.S. *see* Larsen and Higgins, 67 (abs. 23)
HOBBS, S.D. *see* McNabb and Hobbs, 241-245
HOLLABAUGH, C.L., B.D. ROBERTSON and V.L. PURCELL. The petrology and vapor phase mineralogy of rhyolite and tuffs from Garnet Hill, White Pine County, Nevada. 201-210
home ranges
elk: McCorquodale *et al.,* 29-34
HUBERT, W.A. *see* Kozel *et al.,* 175-182
ice
movement and tree wounds: Filip *et al.,* 211-213
snow avalanche-dams: Butler, 109-115
Idaho
bald eagles: Spahr and Bechard, 65 (abs. 13)
bats: Nackenhut and Keller, 65 (abs. 14)
dinoseb in soil: Stevens and Crawford, 70 (abs. 34)
rodents: Keller, 65 (abs. 15)
small mammals: Boone and Keller, 65 (abs. 16)

Jordan
Pinus halepensis growth: Larsen and Higgins, 67 (abs. 23)

KARDONG, K.V. *see* Robinson and Kardong, 71 (abs. 39)
KELLER, B.L. Eight years of data on the relative density and species composition of rodent populations at the Idaho National Engineering Laboratory Site. 65 (abs. 15)
KELLER, B.L. *see* Boone and Keller, 65 (abs. 16)
KELLER, B.L. *see* Wackenhut and Keller, 65 (abs. 14)
KLINKA, K., R.E. CARTER, M.C. FELLER and Q. WANG. Relations between site index, salal, plant communities and sites in coastal Douglas-fir ecosystems. 19-28
knapweed
diffuse (*Centaurea diffusa*)
and grass seedlings: Larson and McInnis, 162-166
squarrose (*C. virgata*)
distribution: Roché and Roché, 246-252
KOZEL, S.J., W.A. HUBERT and M.G. PARSONS. Habitat features and trout abundance relative to gradient in some Wyoming streams. 175-182
KROHN, B. and E.G. BIZEAU. An estimate of bias in tail-fan surveys of Rocky Mountain Canada geese. 1-4

LARSEN F.E. and S.S. HIGGINS. Adaptation of the FOREST-BCG model to warm, dry climates: growth of *Pinus halepensis* in Jordan. 67 (abs. 23)
LARSON, L.L. and M.L. MCINNIS. Impact of grass seedlings on establishment and density of diffuse knapweed and yellow starthistle. 162-166
LARSON, L.L., M.L. MCINNIS, R.F. MILLER and J.A. TANAKA. Forage reduction and seedling emergence by whitetop (*Cardaria draba* (L.)) in the sagebrush ecosystem. 67 (abs. 22)
LARSON, L.L. *see* McInnis *et al.,* 71 (abs. 40)
Leavenworth area, Wa
glacial sequence: Long, 73 (abs. 46)
LEIDHOLT, K.L., W. McCOMB and D.E. HIBBS. The effect of beaver on stream and stream-side characteristics and coho populations in western Oregon. 71 (abs. 37)
LEININGER, W.C., S.H. SHARROW and S.D. RHODES. Sheep production in coastal Oregon Douglas-fir plantations. 195-200
LINDZEY, F.G. *see* Barnhurst and Lindzey, 35-37
LINK, S.O., M.E. THIEDE, R.D. EVANS, J.L. DOWNS and G.W. GEE. Responses of *Artemisia tridentata* and *Grayia spinosa* to increasing seasonal drought. 63 (abs. 7)
LINK, S.O. *see* Evans *et al.,* 66 (abs. 19)
locusts, black (*Robinia pseudo-acacia*)
and groundwater uptake: Rickard and Price, 87-89
LONG, W.A. Reinterpretation of the alpine glacial sequence in the Leavenworth area, Washington. 73 (abs. 46)
LONG, W.A. A probable sixth Leavenworth glacial substage in the Icicle-Chiwaukum Creeks Area, north Cascade Range, Washington. 96-103
LU, S.J. and J.B. ZAERR. Seasonal and diurnal trends of leaf water potential of young red alder (*Alnus rubra*) along a density gradient in western Oregon. 68 (abs. 25)

MacHUTCHON, A.G. Spring and summer food habits of black bears in the Pelly River valley, Yukon. 116-118
MACK, R.N. *see* Novak and Mack, 67 (abs. 21)
MACKELBURG, L.E. and R.W. THORINGTON, Jr. Platyrrine distribution and the theory of corroborating evidence. 72 (abs. 43)
mammals, small
  fauna from Touchet Beds: Spencer, 167-174
  ground squirrels: Betts, 66 (abs. 17); Weddell, 66 (abs. 18)
  Microtus montanus microhabitats: O'Connell and Hallett, 71 (abs. 38)
  pocket gophers: Cox, 77-82
  rodent populations: Keller, 65 (abs. 15)
  and waste disposal: Boone and Keller, 65 (abs. 16)
McANNIS, D. and M.J. BECHARD. Home range and habitat use of ferruginous hawks in the Snake River Birds of Prey Area. 64 (abs. 12)
McCOMB, W. *see* Leidholt *et al.,* 71 (abs. 37)
McCORQUODALE, S.M. Population ecology of a shrub-steppe elk herd. 62 (abs. 4)
McCORQUODALE, S.M., K.J. RAEDEKE and R.D. TABER. Home ranges of elk in an arid environment. 29-34
McINNIS, M.L., L.L. LARSON and M. VAVRA. Hierarchical cluster analysis as an aid for interpreting herbivore diets. 71 (abs. 40)
McINNIS, M.L. *see* Larson and McInnis, 162-166
McINNIS, M.L. *see* Larson *et al.,* 67 (abs. 22)
McNABB, D.H. and S.D. HOBBS. Shallow tillage fails to increase five-year growth of Ponderosa pine seedlings. 241-245
MEAD, B.R. *see* Yarie and Mead, 221-231
methoxylated bibenzyls
  kinetics: Fryxell *et al.,* 73 (abs. 47)
MEYER, S.E. Warm pretreatment effects on antelope bitterbrush (*Purshia tridentata*) germination response to chilling. 146-153
Microtus *see* vole
MILLER, R.F. *see* Larson *et al.,* 67 (abs. 22)
MILNE, D.G., A.S. HARESTAD and K. ATKINSON. Diets of wolves on northern Vancouver Island. 83-86
MISHAGA, R. *see* Halse *et al.,* 154-161
MONDA, M.J. and J.D. REICHEL. Avian community changes following Lower Granite Dam construction on the Snake River, Washington. 13-18
Montana
  bull trout: Fraley and Shepard, 133-143
  snow avalanche-dams: Butler, 109-115
MOODY, M.E. *see* Palmer and Moody, 68 (abs. 26)
Mount Hood, Or
  Devils Kitchen thermal area: Cameron, 73 (abs. 45)
mountain beaver (*Aplodontia rufa*)
  and Douglas-fir damage: Campbell and Evans, 70 (abs. 35)
  nests: Carey *et al.,* 70 (abs. 36)
mountain lions (*Felis concolor*)
  detection: Barnhurst and Lindzey, 35-37

Nevada
  rhyolite and tuffs: Hollabaugh *et al.,* 201-210
NOVAK, S.J. and R.N. MACK. Electrophoretic variability in Washington and British Columbia populations of cheatgrass: evidence for multiple introductions. 67 (abs. 21)

O'CONNELL, M.A. and J.G. HALLETT. Microhabitat selection by *Microtus montanus.* 71 (abs. 38)
Oregon
  bald eagles: DellaSala *et al.,* 104-108
  beaver and fish: Leidholt *et al.,* 71 (abs. 37)
  cattle and conifer seedlings: Doescher *et al.,* 232-240
  great gray owl reproduction: Bull *et al.,* 38-43
  Mount Hood thermal area: Cameron, 73 (abs. 45)
  pocket gophers: Cox, 77-82
  red alder water use: Lu and Zaerr, 68 (abs. 25)
owls
  in Columbia Basin: Fitzner, 63 (abs. 5)
  great gray (*Strix nebulosa*)
    reproduction and mortality: Bull *et al.,* 38-43

PALMER, J.S. and M.E. MOODY. A mathematical model for the spread and control of the AIDS epidemic. 68 (abs. 26)
PANWALA, C.M. *see* Simmons *et al.,* 63 (abs. 6)
PAPENDICK, R.I. *see* Bidlake *et al.,* 69 (abs. 29)
PARKS, C.A. *see* Filip *et al.,* 211-213
PARSONS, M.G. *see* Kozel *et al.,* 175-182
PASSMORE, M.F. and C. BITTLER. Canada goose brooding habitats on the Columbia River between Crow Butte Island and Richland, Washington. 64 (abs. 10)
PASSMORE, M.F. *see* Boe *et al.,* 64 (abs. 11)
Pelly River, Yukon
  black bears: MacHutchon, 116-118
Picea *see* spruce
pines
  Pinus halepensis
    potential growth in Jordan: Larsen and Higgins, 67 (abs. 23)
  ponderosa (*Pinus ponderosa*)
    seedling growth and shallow tillage: McNabb and Hobbs, 241-245
Pinus *see* pines
Placida *see* slug, sea
plant communities
  and salal: Klinka *et al.,* 19-28
plants
  communication
    and W-waves: Wagner, 69 (abs. 32); 119-128
  distribution
    and ecological processes: Simmons *et al.,* 63 (abs. 6)
  spacings
    and W-waves: Wagner, 70 (abs. 33)
pocket gophers, northern (*Thomomys talpoides*)
  food habits: Cox, 77-82
POOLE, L.D. *see* Rickard and Poole, 183-193
PRICE, K.R. *see* Rickard and Price, 87-89
Pseudotsuga *see* Douglas-firs
PURCELL, V.L. *see* Hollabaugh *et al.,* 201-210
Purshia *see* bitterbrush

QUINN, R. Meteorological and hydrological drought in Washington state, 1986-88. 72 (abs. 44)

RADWAN, M.A. Influence of forest floor on growth of Douglas-fir and western hemlock seedlings with and without fertilizer. 68 (abs. 28)
RAEDEKE, K.J. *see* McCorquodale *et al.,* 29-34
rattlesnakes, northwest (*Crotalus viridis*)
  prey location: Robinson and Kardong, 71 (abs. 39)
REICHEL, J.D. *see* Monda and Reichel, 13-18
RHODES, B.D. *see* Leininger *et al.,* 195-200
rhyolite
  from Garnet Hill, Nevada: Hollabaugh *et al.,* 201-210
RICKARD, W.H. Response of round-headed buckwheat to summer burning. 144-145
RICKARD, W.H. and L.D. POOLE. Terrestrial wildlife of the Hanford Site: past and future. 183-193

RICKARD, W.H. and K.R. PRICE. Uptake of tritiated groundwater by black locust trees. 87-89
RICKARD, W.H., Jr. *see* Brandt and Rickard, 64 (abs. 9)
riparian habitats
  and birds: Monda and Reichel, 13-18
rivers
  beavers and streams: Leidholt *et al.,* 71 (abs. 37)
  cold desert spring-streams: Cushing, 62 (abs. 1)
  trout and channel gradient: Kozel *et al., 175-182*
ROBERTSON, B.D. *see* Hollabaugh *et al., 201-210*
Robinia *see* locust, black
ROBINSON, B. and K.V. KARDONG. Methods for relocation of prey for northwest rattlesnake, *Crotalus viridis oreganus.* 71 (abs. 39)
ROCHÉ, B.F., Jr. *see* Roché and Roché, 246-252
ROCHÉ, C.T. and B.F. ROCHÉ, Jr. Introductory notes on squarrose knapweed (*Centaurea virgata* Lam. ssp. *squarrosa* Gugl.). 246-252
rodents
  in Idaho: Keller, 65 (abs. 15)
RODIN, W.A. *see* Fryxell *et al.,* 73 (abs. 47)
ROHWEDER, R.S. *see* Bull *et al.,* 38-43
ROTTINK, B.A. *see* Halse *et al.,* 154-161
RYCHERT, R.C. Toxicity testing using microbial systems. 69 (abs. 30)

sagebrush (*Artemisia tridentata*)
  carbon allocation in drought: Evans *et al.,* 66 (abs. 19)
  response to drought: Link *et al.,* 63 (abs. 7)
sagebrush steppe
  spring flora: Taylor, 63 (abs. 8)
salal (*Gaultheria shallon*)
  and tree growth: Klinka *et al.,* 19-28
Salvelinus *see* trout, bull
SCHULLERY, P. Yellowstone fires: a preliminary report. 44-54
seeds
  seed zone conditions: Bidlake *et al.,* 69 (abs. 29)
SHAINSKY, L.J. *see* Emmingham and Shainsky, 67 (abs. 24)
SHARROW, S.H. *see* Leininger *et al.,* 195-200
sheep, domestic
  and eagles: DellaSala *et al.,* 104-108
  production in Douglas-fir plantations: Leininger *et al.,* 195-200
SHEPARD, B.B. *see* Fraley and Shepard, 133-143
shrub-steppe habitat
  restoration: Brandt and Rickard, 64 (abs. 9)
Sidalcea
  taxonomy: Halse *et al.,* 154-161
SIMMONS, M.A., J.M. THOMAS and C.M. PANWALA. A method for studying the relationship between plant distribution and ecological processes. 63 (abs. 6)
slugs, sea (*Placida dendritica*)
  and algal host: Trowbridge, 72 (abs. 41)
Snake River
  birds and dam construction: Monda and Reichel, 13-18
  Canada geese: Boe *et al.,* 64 (abs. 11)
SPAHR, R.R. and M.J. BECHARD. Factors affecting distribution and foraging of wintering bald eagles on the Boise River in southwestern Idaho. 65 (abs. 13)
species distribution
  and theory of corroborating evidence: Mackelburg and Thorington, 72 (abs. 43)
SPENCER, P.K. A small mammal fauna from the Touchet Beds of Walla Walla County, Washington: support for the multiple-flood hypothesis. 167-174
Spermophilus *see* squirrels, ground
spruce (*Picea* spp.)
  attacked by spruce beetles: Hard, 5-12
squirrels, ground (*Spermophilus*)
  Columbian (*S. columbianus*)
    distribution: Weddell, 66 (abs. 18)
  Washington (*S. washingtoni*)
    range: Betts, 66 (abs. 17)
starthistle, yellow (*Centaurea solstitialis*)
  and grass seedlings: Larson and McInnis, 162-166
Sterna *see* terns
STEVENS, T.O. and R.L. CRAWFORD. The fate of dinoseb (4, 6-dinitro, 2-sec-butyl phenol) in several Idaho soils varying in soil type and exposure history. 70 (abs. 34)
streams *see* rivers
Strix *see* owl, great gray

TABER, R.D. *see* McCorquodale *et al.,* 29-34
TANAKA, J.A. *see* Larson *et al.,* 67 (abs. 22)
taxonomy
  Sidalcea: Halse *et al.,* 154-161
TAYLOR, R.J. Spring flora of the sagebrush steppe, emphasizing ecology and adaptations. 63 (abs. 8)
terns, Forster's (*Sterna forsteri*)
  reproduction: Hall, 90-95
TESCH, S.D. *see* Doescher *et al.,* 232-240
THIEDE, M.E. *see* Link *et al.,* 63 (abs. 7)
THIELMAN, M.J. *see* Benham *et al.,* 73 (abs. 48)
thiram
  and tree damage: Campbell and Evans, 70 (abs. 35)
THOMAS, C.L. *see* DellaSala *et al.,* 104-108
THOMAS J.M. *see* Simmons *et al.,* 63 (abs. 6)
Thomomys *see* pocket gophers
THORINGTON, R.W., Jr. *see* Mackelburg and Thorington, 72 (abs. 43)
TOBIASON, F.L. *see* Benham *et al.,* 73 (abs. 48)
Touchet Beds, Wa
  small mammal fauna: Spencer, 167-174
toxicity testing
  with microbial systems: Rychert, 69 (abs. 30)
trout
  and channel gradient: Kozel *et al.,* 175-182
  bull (*Salvelinus confluentus*)
    in Flathead Lake and river: Fraley and Shepard, 133-143
TROWBRIDGE, C.D. Timing and location of algal host use by an oligophagous marine herbivore. 72 (abs. 41)
Tsuga *see* hemlock
tuffs
  from Garnet Hill, Nevada: Hollabaugh *et al.,* 201-210

understory biomass
  regression approach: Yarie and Mead, 221-231
Ursus *see* bears, black

Vancouver Island
  wolves: Milne *et al.,* 83-86
VAVRA, M. *see* McInnis *et al.,* 71 (abs. 40)
vivianite
  from Olympic Penninsula: Benham *et al.,* 73 (abs. 48)
volcanism
  impacts and extinctions: Carson, 129-131
voles, montane (*Microtus montanus*)
  habitat selection: O'Connell and Hallett, 71 (abs. 38)

W-waves
  and biological clocks: Wagner, 69 (abs. 31)
  and plant communication: Wagner, 69 (abs. 32); 119-28
  and plant spacings: Wagner, 70 (abs. 33)

WACKENHUT, M.C. and B.L. KELLER. Composition, distribution, and movements of bats in southern Idaho. 65 (abs. 14)
WAGNER, O.E. Plant communication and W-waves. 69 (abs. 32)
WAGNER, O.E. Plant spacings and W-waves. 70 (abs. 33)
WAGNER, O.E. W-waves and biological clocks. 69 (abs. 31)
WAGNER, O.E. W-waves and plant communication. 119-128
WANG, Q. *see* Klinka *et al.*, 19-28
Washington
  alpine glacial sequence: Long, 73 (abs. 46); 96-103
  birds and dam construction: Monda and Reichel, 13-18
  Canada geese: Passmore and Bittner, 64 (abs. 10)
  cheatgrass introduction: Novak and Mack, 67 (abs. 21)
  drought, 1986-88: Quinn, 72 (abs. 44)
  Forster's tern: Hall, 90-95
  restoring shrub-steppe: Brandt and Rickard, 64 (abs. 9)
  small mammal fauna: Spencer, 167-174
  vivianite: Benham *et al.*, 73 (abs. 48)
  wildlife: Rickard and Poole, 183-193
waste disposal
  and small mammals: Boone and Keller, 65 (abs. 16)
water uptake
  by black locust trees: Rickard and Price, 87-89
WEDDELL, B.J. Distribution and movement of Columbian ground squirrels (*Spermophilus columbianus*) in uncultivated habitat: are habitat patches like islands? 66 (abs. 18)
whitetop (*Cardaria draba*)
  seedling emergence: Larson *et al.*, 67 (abs. 22)
wildlife
  on the Hanford site: Rickard and Poole, 183-193
Willamette Valey, Or
  eagles and sheep: DellaSala *et al.*, 104-108
wolves (*Canis lupus*)
  diet: Milne *et al.*, 83-86
Wyoming
  trout: Kozel *et al.*, 175-182
  Yellowstone fires: Schullery, 44-45

YARIE, J. and B.R. MEAD. Biomass regression equations for determination of vertical structure of major understory species of southeast Alaska. 221-231
Yellowstone Park, Wy
  fires in 1988: Schullery, 44-54
Yukon
  black bears: MacHutchon, 116-118

ZAERR, J.B. *see* Lu and Zaerr, 68 (abs. 25)

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Once again I express for *Northwest Science* and the Association our special thanks to Caroline Hooper for preparation of the index to volume 63.

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March 1990 Volume 64, Number 2

NORTHWEST SCIENCE

CONTENTS

ABSTRACTS
Sixty-third Annual Meeting
of the
Northwest Scientific Association
March 21-23, 1990
LaSells Stewart Center
Oregon State University
Corvallis, Oregon

65 Program

67 Symposium Schedule and Contributed Papers

91 Abstracts

116 Author Index to Abstracts

118 Key Word Index to Abstracts

120 Acknowledgements

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March 1990 Volume 64, Number 2

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CONTENTS

ABSTRACTS
Sixty-third Annual Meeting
of the
Northwest Scientific Association
March 21-23, 1990
LaSells Stewart Center
Oregon State University
Corvallis, Oregon

65 Program

67 Symposium Schedule and Contributed Papers

91 Abstracts

116 Author Index to Abstracts

118 Key Word Index to Abstracts

120 Acknowledgements

PROGRAM SCHEDULE

NORTHWEST SCIENTIFIC ASSOCIATION
SIXTY-THIRD ANNUAL MEETING

LaSells Stewart Center
Oregon State University

WEDNESDAY, March 21:

7:00-10:00 a.m.	REGISTRATION
8:00 a.m. - 5:00 p.m.	SYMPOSIUM: Environmental Disasters: The Nature of Recovery
7:30 - 10:00 p.m.	Mixing Science and Fun: A Wine and Cheese Social
9:00 - 11:00 p.m.	Board of Trustees Meeting

THURSDAY, March 22:

7:30 - 10:00 a.m.	REGISTRATION
8:00 - 12:00 a.m.	CONTRIBUTED PAPERS:
	Forestry
	Wildlife
	SYMPOSIUM: Science Education Forum: Applied Research: What's Happening in Hands-On Science?
12:00 noon	Field Trip to Finley Wildlife Refuge*
Noon	LUNCH: On your own
1:00 - 5:00 p.m.	CONTRIBUTED PAPERS:
	Forestry
	Botany
	SYMPOSIUM: Our Solar Energy Future in the Pacific Northwest
5:30 p.m.	NWSA SOCIAL HOUR - Elks Lodge
6:30 p.m.	NWSA AWARDS BANQUET - Elks Lodge
	Speaker: David Alt - Giant Meteorite Impact in Southeastern Oregon

FRIDAY, March 23:

8:00 a.m.	All-day Field Trip to Oregon Coast: Marine Science Center* Seafood lunch on waterfront, Newport Return to Corvallis at 5:00 p.m.
8:00 - 12:00 a.m.	CONTRIBUTED PAPERS: Forestry Botany Aquatic Science SYMPOSIUM: Fahnestock Memorial Fire Science Symposium
Noon	LUNCH and NWSA Business Meeting
1:00 - 5:00 p.m.	CONTRIBUTED PAPERS: Forestry Earth Sciences SYMPOSIUM: Lichen Ecology SYMPOSIUM: Fahnestock Memorial Fire Science Symposium
5:00 p.m.	End of Conference

*Load in parking lot between LaSells Stewart and Parker Stadium

SYMPOSIUM

ENVIRONMENTAL DISASTERS: THE NATURE OF RECOVERY

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Wednesday, March 21, 1990

Austin Auditorium

Co-chairs: Mark Wilson, Department of Botany and Plant Pathology, Oregon State University
Nan Vance, PNW Research Station, Corvallis, Oregon

8:00 - 8:15am Welcome and Introduction, Bill Emmingham, Department of Forest Science, Oregon State University

Yellowstone and Other Major Fires

8:15 - 8:45am Ronald H. Wakimoto, University of Montana-The Yellowstone fires of 1988: Natural process and national policy.

8:45 - 9:15am Peter F. Stickney, USDA Forest Service, Missoula-Early development of vegetation following holocaustic wildfire in Northern Rocky Mountain forests.

9:15 - 9:45am Thomas Bonnicksen, Texas A & M University-The Yellowstone wildfire: A restoration ecology perspective.

9:45 - 10:00am Questions

10:00 - 10:30am Break

Alaska oil spill

10:30 - 11:00am Jerry Galt, NOAA, Seattle-Physical processes affecting the movement and spreading of oil from the Exxon Valdez.

11:00 - 11:30am Judith McDowell Capuzzo, Woods Hole Oceanographic Institute-Biological effects of petroleum hydrocarbons: Predictions of long-term effects and recovery.

11:30 - 11:45am Questions

11:45 - 1:15pm Lunch

Alaska earthquake

1:15 - 1:45pm George Plafker, US Geological Survey, Menlo Park-Regional vertical tectonic displacement of shorelines in south-central Alaska during and between great earthquakes.

1:45 - 2:15pm John F. Thilenius, Juneau, Alaska-Ecology of repeated high rate, natural events: Copper River Delta, Alaska.

2:15 - 2:30pm Questions

2:30 - 2:45pm Break

Mount St. Helens eruption

2:45 - 3:15pm James A. MacMahon, Utah State University-Recovery of terrestrial ecosystems at Mount St. Helens: Implications for ecological theory and management.

3:15 - 3:45pm Robert C. Wissmar, University of Washington-Recovery of lakes in the 1980 blast zone of Mount St. Helens.

3:45 - 4:15pm Peter Frenzen, Mount St. Helens National Monument-Eruption impacts and vegetation responses.

4:15 - 4:45pm James Sedell, USDA Forest Service, Corvallis-Confirmation of an old paradigm: The quick recovery of streams in the Mount St. Helens blast zone.

4:45 - 5:15pm Questions

CONTRIBUTED PAPERS

FORESTRY

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Thursday, March 22, 1990

Construction and Engineering Hall

Session Leader: Liz Cole, Department of Forest Science, Oregon State University

8:20 - 8:40am 1 COMPARATIVE GROWTH OF SEEDLING RED ALDER AND WESTERN HEMLOCK GROWING IN PURE AND MIXED STANDS. E. C. Cole and M. Newton. Department of Forest Science, Oregon State University, Corvallis, Oregon 97331-5705.

8:40 - 9:00am 2 PRODUCTION OF QUALITY RED ALDER PLANTING STOCK. M. A. Radwan and W. V. Fangen. USDA For. Serv., and Wash. State Webster Nursery, Olympia, Washington 98502.

9:00 - 9:20am 3 DEVELOPMENT OF THE SIZE-DENSITY SURFACE FOR MIXED RED ALDER/DOUGLAS-FIR STANDS. K. J. Puettmann, D. E. Hibbs, and D. W. Hann. Oregon State University, Corvallis, 97331-5705.

9:20 - 9:40am 4 THE ROLE OF WATER STRESS IN MEDIATING INTRA-SPECIFIC COMPETITION AMONG RED ALDER TREES. P. Giordano and D. E. Hibbs. Oregon State University, Corvallis, Oregon 97331-5705.

9:40 - 10:00am 5 FERTILIZATION AND LIMING OF DOUGLAS-FIR AND NOBLE FIR CHRISTMAS TREES. D. P. Hanley. Washington State University, Pullman, Washington.

10:00 - 10:20am BREAK

10:20 - 10:40am 6 COMPARISON OF EARLY GROWTH AND FORM OF DOUGLAS-FIR PLANTED IN CLUSTER AND GRID PATTERNS. W. Emmingham, S. Sharrow, and J. Entry. Oregon State University, Corvallis, Oregon 97331-5705.

10:40 - 11:00am 7 UNDERSTORY COMPETITION FOR RESOURCES IN PINUS PONDEROSA FORESTS OF NORTHEASTERN OREGON. G. M. Riegel and R. F. Miller. Eastern Oregon Agricultural Research Station, Burns, Oregon 97720.

11:00 - 11:20am 8 PSME: PLANTATION SIMULATOR-MIXED EVERGREEN. T. B. Harrington, J. C. Tappeiner II, and T. F. Hughes. Oregon State University, Corvallis, Oregon 97331-5705.

11:20 - 11:40am 9 STRUCTURAL PATTERNS IN YOUNG JUNIPERUS OCCIDENTALIS. S. Kramer and L. E. Eddleman. Oregon State University, Corvallis, Oregon 97331-5705.

11:40 - 12:00pm 10 ALLOCATION PATTERNS OF CARBON AND MINERALS IN JUNIPERUS OCCIDENTALIS. P. M. Miller, L. E. Eddleman, and S. Kramer. Oregon State University, Corvallis, Oregon 97331-5705.

12:00 - 1:20pm LUNCH

Session Leader: Ted Thomas, College of Forest Resources, University of Washington

1:20 - 1:40pm 11 DYNAMICS OF ATMOSPHERIC DEPOSITION INTO THE HOH RIVER VALLEY OLYMPIC PENIN., WASHINGTON. T. B. Thomas and R. L. Edmonds. University of Washington, Seattle, Washington.

1:40 - 2:00pm 12 A COMPARISON OF TWO METHODS OF ACIDIC DEPOSITION IN CONJUNCTION WITH HEAVY METAL EFFECTS ON SEEDLING DEVELOPMENT OF NORTHERN ROCKY MT. PICEA ENGELMANNII PARRY. L. L. Gilliland and D. J. Bedunah. School of Forestry, University of Montana, Missoula, Montana.

2:00 - 2:20pm 13 EFFECTS OF CO_2 ENRICHMENT ON GROWTH OF ENGELMANN SPRUCE. R. D. Guy and D. Holowachuk. University of British Columbia, Vancouver, Canada.

2:20 - 2:40pm 14 EFFECT OF INCREASED CO_2 AND CLIMATE CHANGE ON TREE GROWTH: PROCESS MODEL. W. L. Webb. Oregon State University, Corvallis, Oregon 97331-5705.

2:40 - 3:00pm 15 PATTERNS OF DECLINE OF ABIES AMABILIS IN OLD-GROWTH STANDS IMPACTED BY TEPHRA DEPOSITION FROM MT. ST. HELENS. G. Segura[1], T. M. Hinckley[1], and G. Wright[2]. [1]College of Forest Resources, University of Washington, Seattle, Washington 98115. [2]USDA-FS, GPNF Randle District, Randle, Washington 98377.

3:00 - 3:20pm BREAK

3:20 - 3:40pm 16 EDGE EFFECTS OF A FOREST ISLAND IN SOUTHEAST ALASKA. J. A. Concannon, P. B. Alaback, and J. F. Franklin. College of Forest Resources, University of Washington, Seattle, Washington 98195 and USFS Forestry Sciences Laboratory, Juneau, Alaska, P.O. Box 20909, 99802.

3:40 - 4:00pm 17 EDGE PHENOMENA: BIOLOGICAL MEASUREMENTS. J. Chen[1], J. Franklin[1], and T. Spies[2]. [1]College of Forest Resources, University of Washington, Seattle, Washington 98195 and [2]USDA-FS, PNW Research Station, 3200 Jefferson Way, Corvallis, Oregon 97331.

4:00 - 4:20pm 18 TREE INVASION DYNAMICS DURING PRIMARY SUCCESSION ALONG TWO RIVERS IN WESTERN WASHINGTON. R. Van Pelt. University of Washington, Seattle, Washington.

4:20 - 4:40pm 19 CANOPY CLOSURE IN YOUNG DOUGLAS-FIR STANDS: AN ECOSYSTEM PERSPECTIVE. J. S. Lowe. College of Forest Resources, University of Washington, Seattle, Washington.

4:40 - 5:00pm 20 SCIENCE, PHILOSOPHY AND THE FOREST SERVICE. J. A. Concannon and K. C. Clatterbaugh. College of Forest Resources and Philosophy Department, University of Washington, Seattle, Washington 98195.

CONTRIBUTED PAPERS

SCIENCE EDUCATION/SOCIAL SCIENCE

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Thursday, March 22, 1990

Agricultural Sciences Room

Session Leader: Gene Craven, Department of General Science, Oregon State University

I. Science Education Forum

APPLIED RESEARCH: What's Happening in Hands-On Science?

8:20 - 9:00am Barbara Middleton, Leader, Forest Education Program, Oregon State University, Corvallis, Oregon.

9:10 - 9:50am Shamm Weston, Leader, Wildlife Education Program, Oregon Department of Fish and Wildlife.

10:00 - 10:40am Bill Hastie, Aquatic Education Program, Oregon Department of Fish and Wildlife.

II. Contributed Papers -- Social Science

10:50 - 11:10am
48 MODELING REGIONAL RECREATION PATTERNS: TOWARD COMPREHENSIVE RECREATION RESOURCE PLANNING IN THE NORTHWEST. D. Hospodarsky. Forest Resources Department, Oregon State University, Corvallis, Oregon 97331.

11:10 - 11:30am
49 ENVIRONMENTAL IMPACTS AND SOCIAL CONFLICT CAUSED BY OFF ROAD VEHICLE USE IN THE ROSLYN-CLE ELUM AREA OF WASHINGTON STATE. E. Phillips. Department of Geography and Land Studies, Central Washington University, Ellensburg, Washington.

CONTRIBUTED PAPERS

WILDLIFE

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Thursday, March 22, 1990

Agricultural Production Room

Session Leader: Dan Edge, Department of Fisheries and Wildlife, Oregon State University

8:20 - 8:40am 41 DNA FINGERPRINTING IN STUDIES OF NATURAL POPULATIONS. S. A. Cummings and J. G. Hallett. Washington State University, Pullman, Washington.

8:40 - 9:00am 42 A COHORT MODEL OF MICROTINE RODENT DYNAMICS. J. G. Hallett and M. A. O'Connell. Washington State University, Pullman, Washington.

9:00 - 9:20am 43 EVALUATION OF THE REPELLENCY OF POWDERED STARLING TO DEER AND MOUNTAIN BEAVERS. D. L. Campbell and J. P. Farley. USDA APHIS S&T, Olympia, Washington.

9:20 - 9:40am 44 TERRESTRIAL VERTEBRATE ABUNDANCES IN RED ALDER (ALNUS RUBRA) FORESTS IN THE OREGON COAST RANGE. C. Chambers, W. McComb, and M. Newton. Department of Forest Science, Oregon State University, Corvallis, Oregon 97331-5705.

9:40 - 10:00am 45 RESULTS OF TWO YEARS OF SPOTTED OWL INVENTORIES IN THE UPPER SKAGIT RIVER DRAINAGE. W. L. Gaines, E. R. Garcia, J. L. Bush, and A. Sprague. U.S. Forest Service, Winthrop, Washington.

10:00 - 10:20am BREAK

10:20 - 10:40am 46 CHANGES IN EPIGEIC SPIDER GUILD STRUCTURE AFTER CLEARCUTTING. J. D. McIver, A. R. Moldenke, and G. Parsons. Department of Entomology, Oregon State University, Corvallis, Oregon 97331.

10:40 - 11:00am 47 CONVERTING SOLAR POWERED CALCULATORS TO DATA LOGGERS. L. R. Askham. Washington State University, Pullman, Washington.

CONTRIBUTED PAPERS

BOTANY

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Thursday, March 22, 1990

Agricultural Production Room

Session Leader: Bruce McCune, Department of General Science, Oregon State University

1:20 - 1:40pm 64 PROPAGULE SOURCES OF REVEGETATION AFTER DISTURBANCE. D. L. Clark and M. V. Wilson. Oregon State University, Corvallis, Oregon 97331.

1:40 - 2:00pm 65 SEED BANKS OF FOUR MICROHABITATS IN ALPINE TUNDRA OF THE OREGON HIGH CASCADES. C. A. Ingersoll and M. V. Wilson. Oregon State University, Corvallis, Oregon 97331.

2:00 - 2:20pm 66 SEED DORMANCY IN ALPINE-SUBALPINE PLANTS. T. N. Kaye. Oregon State University, Corvallis, Oregon 97331.

2:20 - 2:40pm 67 GERMINATION OF WHITETOP (CARDARIA DRABA (L.) DESV.) AND DIFFUSE KNAPWEED (CENTAUREA DIFFUSA LAM.) AS INFLUENCED BY OSMOTIC AND SALT STRESSES. G. Kiemnec and L. Larson. Oregon State University, Corvallis 97331.

2:40 - 3:00pm 68 FIRST-YEAR DEFOLIATION EFFECTS ON WHITETOP (CARDARIA DRABA (L.) DESV.). M. L. McInnis, L. L. Larson, R. F. Miller. Department of Rangeland Resources, Oregon State University, Corvallis, Oregon 97331.

SYMPOSIUM ON SOLAR ENERGY

"Solar Energy Future for the Pacific Northwest"

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Thursday, March 22, 1990

Agricultural Science Room

Symposium Chair: Dr. Clifford Fairchild, Physics Dept., Oregon State University

Speakers and Titles

1:30 - 2:10 p.m.	Dr. William Yerkes, Boeing High Technology Center, "*High Efficiency Solar Cells*"
2:10 - 2:50 p.m.	Mr. David Robison, Pacific Power and Light, "*Solar Electric Resource Assessment*"
2:50 - 3:10 p.m.	BREAK
3:10 - 3:50 p.m.	Mr. Scott Speffel, Eugene Water and Electric Board, "*Solar in the Regional Plan*"
3:50 - 4:30 p.m.	Dr. David McDaniels, Physics Dept., University of Oregon, "*Solar Potential of Oregon*"

CONTRIBUTED PAPERS

AQUATIC SCIENCES

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Friday, March 23, 1990

Agricultural Leader Room

Session Leader: Gary L. Larson, National Park Service, Oregon State University

8:20 - 8:40am
60 REARING ECOLOGY OF JUVENILE STEELHEAD (ONCORHYNCHUS MYKISS) AND HABITAT ANALYSIS OF STEAMBOAT CREEK BASIN, OREGON. J. M. Dambacher. Oregon State University, Corvallis, Oregon 97331.

8:40 - 9:00am
62 STATUS OF FISH POPULATIONS AND MANAGEMENT OF MOUNTAIN LAKES IN THE WESTERN U.S. P. F. Bahls. Oregon State University, Corvallis, Oregon 97331.

9:00 - 9:20am
63 EFFECTS OF STOCKED TROUT IN NATURALLY FISHLESS HIGH MOUNTAIN LAKES OF NORTH CASCADE NATIONAL PARK, WASHINGTON. G. A. Lomnicky, Oregon State University, Corvallis, Oregon 97331.

9:20 - 9:40am
58 WATER QUALITY OF GLACIAL AND NON-GLACIAL STREAMS IN MOUNT RAINIER NATIONAL PARK. G. L. Larson[1], C. Hawkins[2], B. Samora[3], S. Gibbons[3]. [1]National Park Service, Oregon State University, Corvallis, Oregon, [2]Olympic National Park, Port Angeles, Washington, [3]Mount Rainier National Park, Tahoma Woods, Washington.

9:40 - 10:00am
61 TRACKING THE LIMNOLOGICAL RECOVERY OF VOLCANICALLY IMPACTED SPIRIT LAKE, MT. ST. HELENS, WASHINGTON: 1980-1989. D. W. Larson. Corps of Engineers, Portland, Oregon.

10:00 - 10:20am BREAK

10:20 - 10:40am
97 TAXONOMIC STRUCTURE OF PHYTOPLANKTON ASSEMBLAGES IN CRATER LAKE, OREGON. C. D. McIntire and M. Debacon. Oregon State University, Corvallis, Oregon 97331.

10:40 - 11:00am
59 TEMPORARY STREAM COMMUNITIES IN WESTERN OREGON: LIFE HISTORIES OF DOMINANT MAYFLIES AND STONEFLIES. M. Dieterich and N. H. Anderson. Oregon State University, Corvallis, Oregon 97331.

CONTRIBUTED PAPERS

BOTANY

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Friday, March 23, 1990

Agricultural Production Room

Session Leader: Steven Acker, Department of Botany, University of Oregon

8:40 - 9:00am
69 VEGETATION AND FLORA OF MYRTLE ISLAND RESEARCH NATURAL AREA, OREGON. R. L. Thompson. Berea College, Berea, Kentucky.

9:00 - 9:20am
70 RARE PLANT SURVEYS FOR THE KOMA KULSHAN HYDROELECTRIC PROJECT, MOUNT BAKER, WASHINGTON. C. Antieau and C. McShane. Ebasco Environmental, Bellevue, Washington 98004-4405.

9:20 - 9:40am
71 LIFE HISTORY, POPULATION DYNAMICS, AND CONSERVATION STATUS OF CALOCHORTUS NITIDUS (LILIACEAE). S. L. Caicco. P. O. Box 3823, Lacey, Washington 98503.

9:40 - 10:00am
72 THE PRESENCE OF BRACHYPODIUM SYLVATICUM IN MACDONALD-DUNN FOREST. D. M. Leavell and C. J. Hubbard. Oregon State University, Corvallis, Oregon 97331.

10:00 - 10:20am BREAK

10:20 - 10:40am
73 SOMATIC EMBRYOGENESIS FROM IMMATURE EMBRYOS IN MEADOWFOAM (LIMNANTHES ALBA). D. Southworth and S. Kwiatkowski. Southern Oregon State College, Ashland, Oregon.

10:40 - 11:00am
74 MITOCHONDRIAL RESPIRATION IN GREEN ALGAE. H. G. Weger[1], R. D. Guy[1] and D. H. Turpin[2]. [1]Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada and [2]Department of Biology, Queen's University, Kingston, Ontario, Canada.

11:00 - 11:20am 75 PROTEINS UNIQUE TO CELLULAR DESICCATION IN TISSUES OF CONIFERS. N. C. Vance. USDA Forest Service, PNW Research Station, FSL, Corvallis, Oregon 97331.

11:20 - 11:40am 76 THE EFFECT OF DEFICIENCIES OF N, P, K, AND MG ON PHOTOSYNTHETIC GAS-EXCHANGE PARAMETERS IN LEAVES OF HYBRID 11 POPLAR. R. H. Wagner. University of Washington, Seattle, Washington.

11:40 - 12:00pm 77 SAP FLOW AND W-WAVES. O. E. Wagner. Wagner Research Lab, Rogue River, Oregon 97537.

12:00 - 1:20pm LUNCH

CONTRIBUTED PAPERS

BOTANY: LICHEN SYMPOSIUM

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Friday, March 23, 1990

Agricultural Production Room

Session Leader: Bruce McCune, Department of General Science, Oregon State University

1:00 - 1:20pm
78 ANNUAL BRANCHING IN THE LICHEN EVERNIA PRUNASTRI IN OREGON. D. F. Stone[1] and B. McCune[2]. [1]30567 Le Bleu Road, Eugene, Oregon 97405 and [2]Oregon State University, Corvallis, Oregon 97331.

1:20 - 1:40pm
79 LEAD ACCUMULATION IN BRANCH SEGMENTS OF INCREASING AGE IN THE LICHEN EVERNIA PRUNASTRI. B. McCune, Oregon State University, Corvallis, Oregon 97331.

1:40 - 2:00pm
80 MASS TRANSPLANTS OF ARBOREAL LICHENS. K. A. Enns. Victoria, British Columbia, Canada.

2:00 - 2:20pm
81 SAMPLING CANOPY LICHENS. W. C. Denison[1] and S. C. Sillett[2]. [1]Oregon State University, Corvallis, Oregon 97331 and [2]University of Florida, Gainesville, Florida.

2:20 - 2:40pm
82 THE EFFECTS OF AIR POLLUTION ON THE CANOPY LICHEN COMMUNITIES OF OLD-GROWTH DOUGLAS-FIR FORESTS. S. C. Sillett. Reed College, Portland, Oregon.

2:40 - 3:00pm
83 A SURVEY OF LICHENS ON QUERCUS GARRYANA IN THE COLUMBIA RIVER GORGE. J. R. Davis. Carson National Fish Hatchery, Carson, Washington.

3:00 - 3:20pm BREAK

3:20 - 3:40pm 84 ASCUS AND SPORE MODIFICATIONS IN EPIPHYTIC HABITATS. M. Sherwood-Pike. University of Oregon, Eugene, Oregon.

3:40 - 4:00pm 85 INTERSPECIFIC INTERACTIONS AND SPECIES DISTRIBUTIONS IN THE CORTICOLOUS LICHEN COMMUNITY GROWING ON RED OAKS IN NORTHERN MICHIGAN. E. John. University of British Columbia, Vancouver, Canada.

4:00 - 4:20pm 86 ECOLOGICAL AND PHYTOGEOGRAPHICAL DISTRIBUTIONS OF THE LOBATE SPECIES OF LECANORA LICHENS IN NORTH AMERICA. B. D. Ryan. Arizona State University, Tempe, Arizona.

4:20 - 4:40pm 87 LICHENS OF GLACIER NATIONAL PARK, MONTANA. A. M. Debolt. Oregon State University, Corvallis, Oregon 97331.

4:40 - 5:00pm 88 THE RARE LICHENS PROJECT: DETERMINING A CONSERVATION STATUS. S. K. Pittam. Smithsonian Institution, Department of Botany, Washington, DC.

GEORGE FAHNESTOCK MEMORIAL FIRE SCIENCE SYMPOSIUM

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Friday, March 23, 1990
Agricultural Sciences Room

Session Leader: J. B. Kauffman, Department of Rangeland Resources, Oregon State University

8:00 - 8:30am 93 FIRE FREQUENCY EFFECTS ON NATURAL FOREST STRUCTURE IN THE SOUTHERN WASHINGTON CASCADES. A. N. Gray. University of Washington, Seattle, Washington.

8:30 - 9:00am 94 FIRE HISTORY ON TWO SITES IN THE SISKIYOU MOUNTAINS, OREGON. J. K. Agee. University of Washington, Seattle, Washington.

9:00 - 9:30am 95 FIRE SEVERITY AND DAMAGE ON EXTENSIVELY- VERSUS INTENSIVELY-MANAGED LANDS WITHIN THE NORTH FORK FIRE, 1988. P. N. Omi and K. Kalabokidis. Colorado State University, Fort Collins, Colorado.

9:30 - 10:00am TO BE ARRANGED

10:00 - 10:30am BREAK

Session Leader: J. K. Agee, College of Forest Resources, University of Washington

10:30 - 11:00am 96 OVERCOMING THE PARADOX IN MANAGING WILDLAND FIRE. S. F. Arno and J. K. Brown. USDA Forest Service, Missoula, Montana.

11:00 - 11:30am 98 VEGETATION RESPONSE TO A DISRUPTION IN FIRE REGIME: INVASION AND ESTABLISHMENT OF WESTERN JUNIPER IN STEENS MOUNTAIN, OREGON. R. F. Miller. Oregon State University, Corvallis, Oregon 97331.

11:30 - 12:00pm 91 FUEL CONSUMPTION AND FIRE BEHAVIOR ASSOCIATED WITH PRESCRIBED FIRES IN SAGEBRUSH ECOSYSTEMS. D. B. Sapsis and J. B. Kauffman. Oregon State University, Corvallis, Oregon 97331.

12:00 - 1:30pm LUNCH

Session Leader: S. G. Pickford, College of Forest Resources, University of Washington

1:30 - 2:00pm 90 BURNING RATE OF SMOLDERING PEAT. W. H. Frandsen. Intermountain Fire Sciences Laboratory, Missoula, Montana.

2:00 - 2:30pm 89 THE PROCESS OF DUFF BURNOUT. R. E. Martin and J. Scott. University of California, Berkeley, California.

2:30 - 3:00pm 92 COMPARISON OF FUEL CONSUMPTION BETWEEN HIGH-INTENSITY FIRES AND MODERATE-INTENSITY FIRES IN LOGGING SLASH. J. N. Hall, USDA Forest Service, PNW Research Station, Seattle, Washington 98105.

CONTRIBUTED PAPERS

FORESTRY

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Friday, March 23, 1990

Construction and Engineering Hall

Session Leader: Denis Lavender, Department of Forest Sciences, University of British Columbia

8:20 - 8:40am
31 MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF DOUGLAS-FIR, WESTERN LARCH, ENGELMANN SPRUCE, AND LODGEPOLE PINE TO CHANGES IN SOIL MOISTURE POTENTIAL AND LIGHT INTENSITY ON A BURNED, MESIC, SOUTH-EXPOSED SITE WITH TWO LEVELS OF VEGETATION REMOVAL. D. Crampton and D. P. Lavender. University of British Columbia, Vancouver, British Columbia.

8:40 - 9:00am
32 VISIBLE DAMAGE IN WHITE SPRUCE SEEDLINGS AFTER SHORT DAY LENGTH TREATMENT. S. L. Gillies and W. E. Vidaver. Simon Fraser University, Burnaby, British Columbia, Canada.

9:00 - 9:20am
33 ROOT GROWTH IN SPRUCE SEEDLINGS PLANTED AFTER STORAGE: EFFECT OF STORAGE DURATION DEPENDS ON SOIL TEMPERATURE. E. L. Camm and G. Harper. Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada.

9:20 - 9:40am
34 PLANT GROWTH PROMOTING RHIZOBACTERIA FOR CONIFERS. C. P. Chanway. University of British Columbia, Vancouver, British Columbia, Canada.

9:40 - 10:00am
35 EFFECTS OF SOIL TEMPERATURE AND MYCORRHIZAL INOCULATION ON WHITE SPRUCE (PICEA GLAUCA) SEEDLING GROWTH AND PHYSIOLOGY. L. D. Husted. University of British Columbia, Vancouver, British Columbia, Canada.

10:00 - 10:20am BREAK

10:20 - 10:40am 36 EFFECTS OF SHORT PHOTOPERIOD TREATMENTS DURING LATE SUMMER UPON THE HARDINESS AND ABSCISIC ACID CONTENT OF BOREAL FOREST SEEDLINGS. D. P. Lavender, S. N. Silim, and L. Charleson. University of British Columbia, Vancouver, British Columbia, Canada.

10:40 - 11:00am 37 EFFECTS OF A DAILY PHOTOPERIOD DURING COLD STORAGE ON THE PHYSIOLOGY AND GROWTH OF BOREAL FOREST SEEDLINGS. D. P. Lavender, S. N. Silim, and L. Charleson. University of British Columbia, Vancouver, British Columbia, Canada.

11:00 - 11:20am 38 PATTERNS OF COLD HARDENING AND DEHARDENING OF WHITE SPRUCE [PICEA GLAUCA (MOENCH.) VOSS] SEEDLINGS. S. N. Silim, D. P. Lavender, and L. Charleson. University of British Columbia, Vancouver, British Columbia, Canada.

11:20 - 11:40am 39 ENVIRONMENTAL CONTROL OF FROST HARDINESS IN SEEDLINGS OF WESTERN RED CEDAR (THUJA PLICATA D. DON) AND YELLOW CEDAR [CHAMAECYPARIS NOOTKATENSIS (LAMB.) SPACH.]. S. N. Silim, L. Charleson, and D. P. Lavender. University of British Columbia, Vancouver, British Columbia, Canada.

11:40 - 12:00pm 40 EFFECTS OF SEVERAL SITE PREPARATION TECHNIQUES UPON THE SHOOT AND ROOT GROWTH OF WHITE SPRUCE [PICEA GLAUCA (MOENCH) VOSS.] AND LODGEPOLE PINE (PINUS CONTORTA DOUGL.) SEEDLINGS. D. P. Lavender and L. Charleson. University of British Columbia, Vancouver, British Columbia, Canada.

12:00 - 1:20pm LUNCH

Session Leader: Don Minore, PNW Research Station, Corvallis, Oregon

1:20 - 1:40pm 21 RIPARIAN TREE SEEDLINGS, SHRUBS, AND ENVIRONMENT IN THE OREGON COAST RANGE. D. Minore. PNW Research Station, Corvallis, Oregon 97331.

1:40 - 2:00pm 22 SEED CHARACTERISTICS OF BIGLEAF MAPLE (ACER MACROPHYLLUM). J. Zasada. USDA Forest Service, Corvallis, Oregon 97331.

2:00 - 2:20pm 23 COASTAL HEADLAND PLANT COMMUNITY COMPOSITION, STRAIT OF JUAN DE FUCA, WASHINGTON. S. K. Rust. University of Washington, Seattle, Washington.

2:20 - 2:40pm 24 MIXED CONIFER ECOLOGICAL TYPES IN THE CALIFORNIA SIERRA NEVADA. G. L. Benson. USFS Plumas National Forest, Oroville, California.

2:40 - 3:00pm 25 PACIFIC YEW: A FORGOTTEN TREE BECOMES VALUABLE. M. D. Murray. USDA Forest Service, Forestry Sciences Laboratory, Olympia, Washington 98502.

3:00 - 3:20pm BREAK

3:20 - 3:40pm 26 EVALUATING ECOLOGICAL SIGNIFICANCE OF OLD-GROWTH FORESTS. M. H. Huff. USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington.

3:40 - 4:00pm 27 GROWTH AND MORTALITY IN OLD-GROWTH FORESTS: A COMPARISON OF TWO HIGH VOLUME STANDS IN THE PACIFIC NORTHWEST. R. Van Pelt. University of Washington, Seattle, Washington.

4:00 - 4:20pm 28 TRACKING WETWOOD IN STUMPS OF WESTERN HEMLOCK. D. C. Shaw, and J. Arthurs. University of Washington, Seattle, and Washington State Department of Natural Resources.

4:20 - 4:40pm 29 ENVIRONMENTAL SENSITIVITY OF PINUS BRUTIA POPULATIONS FOR TWO GROWTH TRAITS. K. Isik[1], Z. Kaya[1], C. H. Tung[2]. [1]Middle East Technical University, Ankara, Turkey and [2]Science Applications International Corporation, Las Vegas, Nevada.

4:40 - 5:00pm
30

RELATIVE WATER CONTENT, XYLEM PRESSURE POTENTIAL, AND TRANSPIRATION RATE IN RELATION TO DROUGHT RESISTANCE IN SIX DESERT SHRUBS OF NORTHWEST CHINA. Z. Q. Wang[1], J. B. Zaerr[1], Y. C. Cai[2], and X. Liu[2].
[1]Oregon State University, Corvallis, Oregon 97331 and [2]Ningxia Forest Research Institute, Yinchuan, People's Republic of China.

CONTRIBUTED PAPERS

EARTH RESOURCES

LaSells Stewart Center, Oregon State University
Corvallis, Oregon
Friday, March 23, 1990

Agricultural Leader Room

Session Leader: Phil Jackson, Department of Geosciences, Oregon State University

1:00 - 1:20pm
50 REGIONAL SIGNIFICANCE OF THE DRYDEN RHYTHMITES AND DROPSTONES, WENATCHEE RIVER VALLEY, WASHINGTON. W. A. Long. 123 Riverfront Dr., Cashmere, Washington 98815.

1:20 - 1:40pm
51 BEDROCK AS A SOURCE OF WATER FOR SCLEROPHYLL VEGETATION. M. Newton and Z. Wang. Oregon State University, Corvallis, Oregon 97331.

1:40 - 2:00pm
52 A PRACTICAL ASSESSMENT OF THE WETLAND EVALUATION TECHNIQUE (WET) AS A TOOL FOR MEETING OREGON'S LAND USE PLANNING GOAL FIVE REQUIREMENTS. J. A. Griffith and P. L. Jackson. Oregon State University, Corvallis, Oregon 97331.

2:00 - 2:20pm
53 COMPARISON OF PRESETTLEMENT AND PRESENT OLD-GROWTH FOREST COMMUNITIES IN THE SHAWNEE HILLS, ILLINOIS. F. B. Crooks. Oregon State University, Corvallis, Oregon 97331.

2:20 - 2:45pm
54 IMAGE BASED SOIL FAUNA TAXONOMY USING HYPERCARD ON A MACINTOSH COMPUTER. C. H. Shaw., A. Moldenke, and J. R. Boyle. Oregon State University, Corvallis, Oregon 97331.

2:45 - 3:15pm BREAK

3:20 - 3:40pm
55 INTERACTION OF W-WAVES AND GRAVITY. O. E. Wagner. Wagner Research Lab., Rogue River, Oregon 97537.

3:40 - 4:00pm 56 THE EFFECT OF TEMPERATURE, MOISTURE AND SOIL ACIDITY ON LIGNIN AND CELLULOSE DECOMPOSITION IN FOREST SOILS. J. A. Entry, P. K. Donnelly, D. L. Crawford, and K. Cromack, Jr. Oregon State University, Corvallis and University of Idaho, Moscow.

4:00 - 4:20pm 57 DISTRIBUTION OF NUTRIENTS AND TRACE METALS IN THE PROFILES OF SOILS AMENDED WITH MUNICIPAL SEWAGE SLUDGE AFTER 15 YEARS. D. Xue, R. Harrison, and C. L. Henry. University of Washington, Seattle, Washington.

1

COMPARATIVE GROWTH OF SEEDLING RED ALDER AND WESTERN HEMLOCK GROWING IN PURE AND MIXED STANDS. E.C. Cole and M. Newton, Oregon State Univ., Corvallis.

Competitive interactions of western hemlock and red alder, growing with and without the presence of salmonberry and other species, were compared on three sites within the Oregon Coast Range. Study design used a combination of Nelder design and replacement series, with five ratios of hemlock to alder--100:0, 75:25, 50:50, 25:75, and 0:100. Densities ranged from 1284 to 85470 trees/ha. On the average, third-year height of hemlock was 40 cm less and height of alder 80 cm less when growing in salmonberry. Third-year volume growth of alder and hemlock was 3.4 times greater in the absence of salmonberry. Overall, height and average standing volume of alder were 2 and 10 times greater than hemlock. Within species, average growth varied by ratio and density. For both species, volume growth was negatively correlated with percent salmonberry cover, percent overtopping, and density.

2

PRODUCTION OF QUALITY RED ALDER PLANTING STOCK. M. A. Radwan and W. V. Fangen. USDA For. Serv., and Wash. State Webster Nursery, Olympia, WA 98502.

Tests were conducted at the Webster Nursery in western Washington to assess different methods for producing red alder planting stock. Seed was sown at different times in flats and styroblocks kept in a greenhouse and in nursery beds with and without cover. Transplant and non-transplant trees were produced, and all stock was lifted in the winter, 9-10 months from sowing. Height, diameter and shoot and root dry weights of the trees were determined. In general, the "plug" trees were the smallest (ca. 27 cm, 0.5 g ea). Very good bare-root trees (ca. 54 cm, 10 g ea) were obtained by direct sowing in the nursery. Sowing in styroblocks and transplanting to nursery beds produced the best stock. Transplants were the largest trees (ca. 78 cm, 25 g ea) with compact, broom-like roots and many root tips. These trees would be easier to outplant and may have higher survival rates than the non-transplant trees with their coarse, irregular roots.

3

DEVELOPMENT OF THE SIZE-DENSITY SURFACE FOR MIXED RED ALDER/DOUGLAS-FIR STANDS. K. J. Puettmann, D. E. Hibbs, and D. W. Hann, Oregon State University, Corvallis.

Data from long-term remeasurements were used to develop size-density trajectories for pure red alder and Douglas-fir stands. The concept was expanded to a size-density surface for pure and mixed red alder/Douglas-fir stands. The Douglas-fir trajectory lies higher than the red alder trajectory. The surface is near linear at higher proportion of red alder and increased curvilinear towards the Douglas-fir trajectory as proportion of Douglas-fir increases. This surface can be used as a maximum to calculate a density index for mixed stands. An investigation into the dynamics underlying the surface showed that at older stands develop toward an increasing Douglas-fir component. Thus they never reach a linear part on their self-thinning trajectory, but shift laterally across the curvilinear surface.

4

THE ROLE OF WATER STRESS IN MEDIATING INTRASPECIFIC COMPETITION AMONG RED ALDER TREES. P. Giordano and D.E. Hibbs. Oregon State Univ., Corvallis.

To examine the role of water stress in mediating the effects of competition on growth of red alder trees, concurrent measures of growth characteristics and predawn water stress were recorded at 2 week intervals for red alder trees growing in the Oregon Coast Range Mountains. The relationship between relative growth rate and water stress suggested a threshold water stress level of -0.3 MPa above which growth was small and was not affected by further increases in water stress. Changes in light availability as competition increased, interacted with this water stress response. The upper canopy was more tolerant of water stress than the lower canopy.

5

FERTILIZATION AND LIMING OF DOUGLAS-FIR AND NOBLE FIR CHRISTMAS TREES. Donald P. Hanley, Washington State University, Pullman, WA.

Douglas-fir and noble fir Christmas trees in Western Washington were treated with fertilizer and lime in order to study the impacts of the treatments and their interactions on tree vigor and current season needle mass. A randomized complete block design was used with 4 locations, 6 fertilizer/lime treatments, and 3 replications at each location for both Douglas-fir and Noble fir. Treatments included lime, 21-0-0, and 10-20-20, each at two application rates. Study statistics that could be observed by growers were selected and included tree height increment, as an indicator of tree vigor, and current season needle weight, as an indicator of tree fullness. Fourth year results indicated an overall weak statistical significance to the fertilizer/lime treatments for Douglas-fir; a strong influence as to field locations; and a significant but weak association between lime and needle weight for Noble fir. Foliar analysis is planned for the future.

6

COMPARISON OF EARLY GROWTH AND FORM OF DOUGLAS-FIR PLANTED IN CLUSTER AND GRID PATTERNS. W. Emmingham, S. Sharrow and J. Entry, Oregon State Univ., Corvallis.

Douglas-fir seedlings were planted in clusters and conventional grid patterns to determine if planting methods altered growth form, moisture deficit and wildlife damage. Trees in the grid planting were at a spacing of 2.44 m. Six trees were planted in a circular cluster 2.2 m in diameter; clusters were 7.7 m apart. Trees planted in cluster patterns had greater height and diameter growth, a lower moisture deficit and less damage due to wildlife browsing than trees planted in grid patterns. After 9 years, trees in clusters had less taper than those in the grid. Our results indicate that planting trees in cluster patterns may be a more appropriate method of regenerating some sites than planting trees in the conventional grid pattern, particularly where low intensity management is planned and final crop tree spacing is important.

7

UNDERSTORY COMPETITION FOR RESOURCES IN PINUS PONDEROSA FORESTS OF NORTHEASTERN OREGON. Gregg M. Riegel, and Richard F. Miller, Eastern Oregon Agric. Res. Sta., Burns, OR 97720

Understory species composition and aboveground biomass production in a ponderosa pine (Pinus ponderosa)/snowberry (Symphoricarpos albus) plant community were altered by supplementing light, water, and nutrients. Twenty-four plots (4x4 m) were trenched one meter in depth, and 24 non-trenched plots were used to asses the effects of tree root competition on vegetation under varying light conditions. Overstory conifers were thinned from 345 to 148 trees/ha $^{-1}$ spacing on half of the plots to increase light levels. Two years after treatment, density of graminoids and forbs increased, while shrub cover decreased as a result of increased light levels in thinned sites. Cover and density of graminoids, forbs, and shrubs increased when soil moisture and nutrient competition with the overstory were controlled in the trenched treatment. Competition for water and nitrogen had a greater impact on understory biomass production than increased light levels. Species response to treatment effects can be correlated to a change in either canopy effected attributes (light, midday air temperature, and soil temperature) or root competition effected attributes (soil water potential, pH, and nitrogen).

8

PSME: PLANTATION SIMULATOR - MIXED EVERGREEN. T.B. Harrington, J.C. Tappeiner II, and T.F. Hughes, Oregon State Univ., Corvallis.

How do sprouting tanoak (Lithocarpus densiflorus) or Pacific madrone (Arbutus menziesii) affect the development of a Douglas-fir (Pseudotsuga menziesii) plantation? Such a question now can be answered with PSME, a computerized growth model that integrates information from seven years of competition research in southwestern Oregon by the Fundamental FIR program. Using inputs of either initial cover in hardwood sprouts or pre-harvest hardwood basal area and density, the model simulates annual cover development for tanoak, madrone, or chinkapin. In each year of the simulation, predicted hardwood cover limits growth of Douglas-fir and understory vegetation based on current research information. At the end of the simulation, Weibull functions provide a description of the distribution of tree sizes for the Douglas-fir population at an age of ten years. PSME is currently being reviewed and verified, and completion is expected in early summer, 1990.

9

STRUCTURAL PATTERNS IN YOUNG JUNIPERUS OCCIDENTALIS. S. Kramer and L.E. Eddleman, Oregon State Univ., Corvallis.

Whole tree excavation of 41 western juniper (Juniperus occidentalis) trees in central Oregon was used to assess the structural changes in root and shoot components of individuals ranging in age from 2 to 34 years. Root biomass allocation shifted from tap to lateral with age. Lateral roots emerged primarily from a zone on the tap root located 5 to 20 cm below the soil surface. Lateral roots dominate in trees >10 years old. Foliage biomass was consistently high at all ages with the transition from juvenile to adult foliage beginning at about 17 years. Root/shoot ratios varied greatly in trees <7 years old, while for those >7 years old R/S ratios ranged from 0.53 to 0.87. Fine root/foliage ratios declined with age from 4.38 downward to 0.85. Tree age and height were strong predictors of biomass components.

10

ALLOCATION PATTERNS OF CARBON AND MINERALS IN JUNIPERUS OCCIDENTALIS. P. M. Miller, L. E. Eddleman, S. Kramer, Oregon State Univ. Corvallis

Biomass, gross heat of combustion, concentrations of macro- and micronutrient elements, and construction costs were measured on above and below-ground tissue of juvenile and small-adult Juniperus occidentalis to understand allocation patterns. Adult foliage had the highest heat of combustion, nitrogen concentration, and construction cost. The relatively high nutrient status of J. occidentalis may indicate that additional root biomass is not required to balance the activity and relative growth rate of above-ground tissue. Juniperus occidentalis had high root:shoot ratios compared to other conifer species from more mesic habitats and Larrea tridentata from more xeric habitats. Compared with similar-aged species for which data are available, juvenile and small-adult J. occidentalis allocate larger proportions of dry mass to foliage, to optimize photosynthetic capacity and to roots, to optimize water and nutrient acquisition; the larger allocation to foliage and roots was accomplished through reduction of allocation to branch/trunk.

11

DYNAMICS OF ATMOSPHERIC DEPOSITION INTO THE HOH RIVER VALLEY, OLYMPIC PENIN.,WA. T.B.Thomas and R.L. Edmonds, Univ. of WA Seattle, Washington

The Hoh River valley encompasses major forest types from alpine to coastal. Precipitation into the Hoh valley forests comes directly off the Pacific and is dominated by sea salts;Na, Cl, SO_4, & Mg. Samples collected from a 30 km transect from the Pacific Ocean heading inland had changes in amount and chemistry of rainfall as it moved away from the Pacific. Precipitation amounts increased with increasing distance from the Pacific, while H^+, NO_3, and SO4 concentration decreased. Sulfate deposition was higher than expected for a remote site, elevated by biogenic production of reduced sulfur in the upper layers of the near-coastal Pacific. Sulfate had seasonal trends with peaks in spring and fall, closely corresponding to peaks in dimethylsulfide production. pH varied little by season or precipitation amount, however, pH was higher 80% of the time at sites farthest from the Pacific. The forest ecosystem and surface waters of the Hoh valley are well-buffered from acidic inputs, and show no sign/symptom of decline or mortality related to acid deposition.

12

A COMPARISON OF TWO METHODS OF ACIDIC DEPOSITION IN CONJUNCTION WITH HEAVY METAL EFFECTS ON SEEDLING DEVELOPMENT OF NORTHERN ROCKY MT. PICEA ENGELMANNII PARRY.L.L. Gilliland and D.J. Bedunah. School of Forestry, U. of Montana, Missoula.

Two types of acidic deposition, total saturation and fog were compared analyzing a) differences between pH levels 2,3.5 and ambient 5.4 b)three heavy metal concentrations of Pb, Cu, Ni and Mn as a group and in conjunction with the levels of acidity and c) the amount of heavy metal uptake by needles. Total saturation was achieved by immersing 2/0 seedlings' needles and stems. A comparable age group was fogged using a low pressure nozzle capable of generating an average droplet size of 12 microns at 20 psi. Treatment length was 2 months, 3 times a week, 4 hours duration. Preliminary results indicate the fog treatment to be more damaging at the pH 2 and 3.5 levels than total immersion. Growth and ICAP analyses are in progress.

13

EFFECTS OF CO_2 ENRICHMENT ON GROWTH OF ENGELMANN SPRUCE. R.D. Guy and D. Holowachuk, University of British Columbia, Vancouver, Canada.

Engelmann spruce (Picea engelmannii Parry) seedlings were grown from seed for 180 days in growth chambers with ambient (340 $\mu L\ L^{-1}$) and CO_2 enriched (1000 $\mu L\ L^{-1}$) air. Reciprocal transfers between treatments took place at 60 and 120 days. Photoperiod was reduced at 100 days to induce bud dormancy. Relative growth rate was most positively affected during the first 60 day period; but absolute growth after 120 days was the same whether enrichment was from days 0 to 60 or from days 60 to 120. Final growth was greatest with continuous enrichment. Shoot to root ratio decreased steadily throughout the experiment and was unaffected by CO_2 enrichment. This was true even when CO_2 was applied after bud set, when shoot sink strength was expected to be minimal. Number of stomata per unit length of needle was also unaffected by CO_2 enrichment.

14

EFFECT OF INCREASED CO2 AND CLIMATE CHANGE ON TREE GROWTH: PROCESS MODEL. Warren L. Webb. Oregon State University, Corvallis.

Increased atmospheric CO2 and climate change are expected to alter forest primary production. A carbon model linking relevant growth physiological processes has been constructed, and includes gross photosynthesis, growth and maintenance respiration, stomatal conductance, carbon allocation and photosynthate conversion into biomass. Submodels that convert crude meteorological station data into high resolution abiotic data are used to drive the model.

The net photosynthesis sections of the model are verified with independent data sets, and simulated growth of Douglas-fir seedlings is within 10 percent of observed growth.

15

PATTERNS OF DECLINE OF *ABIES AMABILIS* IN OLD-GROWTH STANDS IMPACTED BY TEPHRA DEPOSITION FROM MT. ST. HELENS. G.Segura[1], T.M. Hinckley[1], and G.Wright[2]. [1] Coll. of For. Res., Univ. of Wash. Seattle, WA 98115. [2] USDA-FS, GPNF Randle Dist. Randle, WA 98377.

Tephra deposition from the 1980 eruption of Mt. St. Helens affected many mature and old forests of mixed conifer species in southwest Washington. The primary effect of this disturbance is growth loss and/or mortality of of *Abies amabilis* (Doug.)Forbes. Patterns of decline and mortality were investigated in the tephra impacted area. Thirty-six permanent plot installations were stratified across a range of mature and old-growth forests and a range of previously rated *A. amabilis* tephra damage classes. Plot distribution covered a range of distance from the mountain, elevation, and slope position. Decline and mortality were extremely variable among stands despite relatively constant levels of tephra deposition. Declining stands occur mainly in areas that received the finest tephra deposits (Layer A of silt-sized materials). Rate of decline and percent mortality do not appear to be related to site factors such as elevation, slope position, distance from the mountain, habitat type, and site index, but rather to the biological conditions of individual stands prior to the disturbance. Vigor, estimated both at the tree and stand level, appears to be the most important factor determining decline intensity and the ability of trees to recover from this perturbation. The most important variables used to directly or indirectly estimate vigor include species composition; stand age, density, structure, history; and radial growth loss, and other measurements of individual tree crown size.

16

EDGE EFFECTS OF A FOREST ISLAND IN SOUTHEAST ALASKA, Concannon, J.A, P.B. Alaback and J.F. Franklin. Coll. of For. Res., Univ. of Wash., Seattle, WA 98195 and U.S.F.S. For. Science Lab., Juneau, AK, P.O. Box 20909, 99802

Forest fragmentation in Southeast Alaska, caused by logging, can produce isolated forest patches. These patches have a large amount of edge area. The objective of this study was to relate changes in microclimate with forest composition and function, moving into the patch center. A small isolated patch of Tsuga heterophylla, created by logging (135mx250m) was selected on Chichacoff Island near Salt Lake Bay, to characterize edge effects. Air, soil and litter temperatures were measured at 5 locations (clearcut, 5m, 15m, 40m and 75m) into the forest patch, for 5 weeks during the summer of 1989. Biological measurements of plant cover and filter paper decomposition were taken to provide an inference of the edge's influence on species composition and function. The large amount of edge area around this forest island influenced forest microclimate and consequently, plant cover and decomposition.

17

EDGE PHENOMENA: BIOLOGICAL MEASUREMENTS. Chen[1], Jiquan, Jerry Franklin[1], and Thomas Spies[2]. [1] Coll. of For. Res., Univ. of Wash., Seattle, WA 98195 and [2] USDA-FS, PNW Research Station, 3200 Jefferson Way, Corvallis, OR 97331.

Forest edge is one of the most obvious features in the Pacific Northwest landscape. As a part of our research project on edge effects, which also includes physical environment and model simulations, this study focusses on the patterns of several biotic features at the edges of Douglas-fir (Pseudotsuga menziesii) stands. Twenty edges have been selected in the H. J. Andrews (OR) and Wind River (WA) Experimental Forests to look at the patterns of growth, regeneration, mortality, and stand density. Edge exposures (orientations) and distances from cutting boundary into the interior forest are assumed as primary factors influencing the magnitude and range of edge effects. Significant biological effects have been found within 120 m of forest edges, including higher growth rates of Douglas-fir and western hemlock (Tsuga herterophylla), abundant regeneration of Douglas-fir and western hemlock, reduced regeneration of Pacific silver fir (Abies amabilis), higher tree mortality, and lower stand density and basal areas. A simple mathematical model has been developed to evaluate the importance of edge effect at both the stand and landscape levels. We have concluded that forest structure and function at edges are significantly different from interior forest due to surrounding clearcuts. Although affected edge area is often ignored, it is an important element to consider in highly fragmented landscapes.

18

TREE INVASION DYNAMICS DURING PRIMARY SUCCESSION ALONG TWO RIVERS IN WESTERN WASHINGTON. Robert Van Pelt, University of Washington, Seattle.

Primary succession on fresh alluvial sites was examined during the fall and winter of 89-90 along the Dosewalips River in the eastern Olympic Mountains (drainage area 75 sq. mi.) and the Suiattle River in the Northern Cascades (200 sq. mi.). Intensive sampling consisted of 98 plots on nine surfaces between 0-30 years of formation age. Salix and Populus were present within a year of the surface formation on sites that spend several months of the winter under water. Alnus and conifers colonized within 3 years, often after the surface had built up to 1 m above low flow. The slow, initial (2-3 year) growth of Salix and Populus allows for rapid overtopping by Alnus within a few years. Conifers consistently (85% constancy) establish before crown closure. Pseudotsuga are most common at this stage, followed closely by Abies grandis with Thuja and Tsuga heterophylla occasionally present. Herbaceous species played little or no role until trees were well established. Upon the formation of Alnus thickets Pseudotsuga is largely gone, although occasional individuals can still be found in dense thickets. Other coniferous species survive through this stage. When the sites reach 20 years Populus are much taller than other species and Abies grandis and Pseudotsuga are adding height growth rapidly. Frequent flooding and the creation of small temporary side channels transforms what was a homogeneous surface into a mosaic of age classes. Exclusion of conifers by dense Alnus stands was not observed as it has been on other sites in other areas. Larger river systems may be necessary for this phenomenon.

19

CANOPY CLOSURE IN YOUNG DOUGLAS-FIR STANDS: AN ECOSYSTEM PERSPECTIVE. J. Stephen Lowe, Coll. of For. Res., Univ. of Wash., Seattle, WA.

The period of canopy closure is one of the most dynamic times in the natural development of a forest stand. In Douglas-fir ecosystems dramatic changes in the composition, structure, and function are expected. Historically, stand closure has been defined as an event in the development of forests. In this paper I expand the definition to consider a continuum of ecosystem processes. Anticipated changes include alteration of the forest floor environment, shifts in the composition and structure of the understory vegetation, effects on nutrient cycling and productivity, and biomass accumulation and distribution. Characteristic patterns of change during canopy closure occur across a range of spatial and temporal scales. Wider spaced plantings or early precommercial thinnings are management alternatives which could postpone or eliminate canopy closure.

20

SCIENCE, PHILOSOPHY AND THE FOREST SERVICE, Concannon, J.A. and K.C. Clatterbaugh. Coll. of For. Res. and Phil. Dept., Uni. of Wash., Seattle, WA 98195.

U.S. Forest Service scientists have been influenced by two major bodies of philosophy, critical positivism and deep ecology. Critical positivism influenced deterministic scientists whereas deep ecology gave rise to holistic ecosystem analysis. Determinism was prevalent in the early history of the Forest Service when production was the most important aspect of management. Determinism however, narrowed the forester's understanding of a complex forest ecosystem. Deep ecologists, challenged deterministic approaches and provided better insights into explaining forest structure, function and composition. The objective of this talk is to trace the different philosophies of the Forest Service scientists and link them to management policies which are the result of the agency's scientific research. A paradigm shift is occurring in the Forest Service Science Research Unit as a result of the political and scientific acceptance of the ecological approach.

21

RIPARIAN TREE SEEDLINGS, SHRUBS, AND ENVIRONMENT IN THE OREGON COAST RANGE. D. Minore, PNW Research Station, Corvallis, OR.

Tree seedlings, shrub cover, and physiography were studied on riparian areas in the Oregon Coast Range to relate stream characteristics and environment to forest regeneration. Twenty-two streams between Hebo and Gold Beach were measured. Number of tree seedlings was positively correlated with stream gradient, distance from the stream, and time since disturbance; negatively correlated with overstory canopy, latitude, and shrub cover. Shrub cover was positively correlated with latitude and stream width; negatively correlated with distance from the ocean, overstory canopy, overstory basal area, slope, and elevation above the stream. Forest regneration was sparse, and a shrub climax is probable in many coastal riparian areas.

22

SEED CHARACTERISTICS OF BIGLEAF MAPLE (ACER MACROPHYLLUM). John Zasada, USDA Forest Service, Corvallis.

Seed characteristics, germination at 1°C, and changes in viability during storage were studied for seeds collected from 6 Oregon Coast Range sites near Corvallis prior to the start of dispersal and the onset of fall rains. Dry weight ranged from 0.11 to 0.21 g/seed. Embryo dry weight ranged from 31-45 % of seed dry weight. Embryo and seed coat moisture content (% dry weight) varied from 11-75 and 4-32%. Seed germination started after 30 days, and continued through 120 days with a small percentage of seeds still dormant at 120 days. Maximum germination was at 60 or 90 days and varied among trees. The viability of seeds stored at 2°C declined by about 10% over 12 months while those at -10°Cdeclined by about 60%. If bigleaf maple seed is to be stored it should be collected prior to the onset of fall rains which result in increased moisture content and a more rapid decline in viability.

23

COASTAL HEADLAND PLANT COMMUNITY COMPOSITION, STRAIT OF JUAN DE FUCA, WASHINGTON. S. K. Rust, University of Washington, Seattle.

Plant community composition was investigated at Iceberg Point, a coastal headland of the Strait of Juan de Fuca, Washington. Forty sample plots were located on the 22 ha study site by a stratified-random method which employed systematic stratification. Detrended correspondance analysis (DCA) of the cover data results in a primary axis which corresponds to site exposure and represents one full species turnover. DCA axis 2 influences the ordination of exposed sites; but has little influence on the ordination of protected sites. Representing one and one-half species half changes, axis 2 corresponds to the abundance of species tolerant to sea salt spray. DCA axis 3 influences the ordination of protected sites and corresponds to disturbance history. Environmental stress peculiar to the site may give rise to high species diversity and unique species assemblages.

24

MIXED CONIFER ECOLOGICAL TYPES IN THE CALIFORNIA SIERRA NEVADA. G.L. Benson, U.S.F.S., Plumas National Forest, Oroville.

An ecological classification system based on potential natural vegetation and soils is being developed for the Mixed Conifer forests of the northern, central Sierra Nevada in California. This classification is based on stands sampled in the Lassen, Plumas, Tahoe and Eldorado National Forests. These forest stands are dominated by Douglas-fir (Pseudotsuga menziesii), white fir (Abies concolor), ponderosa pine (Pinus ponderosa) or Jeffrey pine (P. Jeffreyi), sugar pine (P. lambertiana) and incense-cedar (Calocedrus decurrens). A hierarchical taxonomic classification of mixed conifer ecological types is being developed using TWINSPAN, DECORANA for vegetation, followed by analysis and correlation with environmental/soils data. The tree, shrub, forb dominants or indicator species and pertinent environmental/soil factors are presented for selected ecological types.

25

PACIFIC YEW: A FORGOTTEN TREE BECOMES VALUABLE. M. D. Murray. USDA Forest Service, Forestry Sciences Laboratory, Olympia, WA 98502.

Pacific yew (Taxus brevifolia), a little known conifer of the Pacific Northwest, has now become valuable. The wood is used for specialty products and bark extractives are believed to be useful in possible treatment of cancer. The ecology and management of this shade-tolerant, slow-growing tree is unknown. Pacific yew grows as understory in dense old-growth stands but can also occur in young stands. Straight, vigorous trees 4 cm dbh, 3 m tall and 40 years old 10 cm above ground were found in a 48-year-old Douglas-fir plantation. In addition, seedlings were found in a 70-year old Douglas-fir stand 6 years after thinning. Asexual regeneration is common and vegetative reproduction may be a way to propogate yew. Growth rate of seedlings and rooted cuttings in various environments, recovery of trees after release, and comparative growth in shaded and unshaded conditions need to be known if yew is to be utilized to its full potential.

26

EVALUATING ECOLOGICAL SIGNIFICANCE OF OLD-GROWTH FORESTS. M.H. Huff USDA Forest Service, Pacific Northwest Research Station, Olympia, WA.

To identify which patches of old forest to retain is a desired and immediate goal of resources management in the Pacific Northwest. Characteristics used to determine a stand's ecological value is divided into three areas of concern: (1) stand structure and degree of old-growthness, (2) landscape characteristics, and (3) plants and animals associated with old-growth forests. The evaluation system to rate various old growth stands is designed to be flexible in order to accommodate potential inequities in amount of information available. The process is based on both quantitative and qualitative assessments relative to management objectives. Examples from within the Western Hemlock Zone of Washington and Oregon are given to demonstrate the evaluation procedure and to suggest some strategies that could be adopted.

27

GROWTH AND MORTALITY IN OLD-GROWTH FORESTS: A COMPARISON OF TWO HIGH VOLUME STANDS IN THE PACIFIC NORTHWEST. Robert Van Pelt, University of Washington, Seattle.

In 1972 an IBP study located two forest stands that were determined to have the highest recorded biomass for their species - Pseudotsuga menziesii (450 years old) growing on a Tsuga heterophylla/Oxalis oregana association in the Central Oregon Cascades and an Abies procera stand (330 years old) on a Abies amabilis/Oxalis-Streptopus rosea association near Mt. St. Helens in southern Washington. Both stands had permanent plots established in 1977 that were 1.2 ha and 4 ha, respectively. Remeasurement of both occurred in 1989. Initial 1977 overstory volumes were 2533.8 m3/ha for the Pseudotsuga stand and 2886.3 m3/ha for the Abies procera stand. Overstory growth in 12 years is 114.5 m3/ha while mortality removed 92.6 m3/ha of this for the Pseudotsuga stand. Equivalent values for the Abies stand are 122.8 m3/ha and 241 m3/ha. Overstory mortality for the Abies stand averaged 6 dominants per ha, of which 75% were Abies procera. Individual growth of dominants is still high in both stands several individuals putting on .85 m3 (Pseudotsuga) and .91 m3 (Abies) every year. Lower tree strata had unexpected trends. Contrary to popular successional theory the component of Tsuga has decreased in the Pseudotsuga stand due to high mortality while only 2 Pseudotsuga trees died in 12 years (0.22%/yr). The Abies procera are nearing the upper limit of their life span and are expected to continue to decrease in importance and in standing volume. The Pseudotsuga in both stands is vigorous and continuing to gain volume although no recruitment occurred in either stand.

28

TRACKING WETWOOD IN STUMPS OF WESTERN HEMLOCK. D.C. Shaw, University of Washington, Seattle, and J. Arthurs, Washington State Department of Natural Resources.

Wetwood is common in the interior butt sections of young-growth (35 yr.) western hemlock. Decay fungi are not present in this wetwood. Wetwood is thought to aid in host defense againt wood decay. We tracked wetwood from ground level down into the roots of 10 western hemlock stumps. We found the stain led to wound scars, callous tissue and compartmentalization lines without decay fungi present in five stumps and led to active decay infections in five stumps.

29

ENVIRONMENTAL SENSITIVITY OF PINUS BRUTIA POPULATIONS FOR TWO GROWTH TRAITS. K. Isik and Z. Kaya, Middle East Technical Univ., Ankara, Turkey, C.-H. Tung, Science Applications International Corporation, Las Vegas, Nevada

Six Pinus brutia Ten. populations (Sarilar, Doyuran, Murtbeli, Bük, Kapan, Hacibekir) from different origins were planted in four common garden experiments located at various elevations on the Tourus Mts. near Antalya, southern Turkey. Tree height and numbers of growth cycles at the sixth growing season were measured, and the "environmental sensitivity" were calculated. The "environmental value" of each common garden as well as the "population value" of each population in each common garden were determined. The regression coefficient for these two variables was then used as the measure of environmental sensitivity. Murtbeli population, a mid-elevation population, had the highest sensitivity. This population also showed the highest population mean among all population studied. In cases where populations or genotypes show similar sensitivities, the breeder should select and breed those populations or genotypes with higher sensitivity values, provided that maladaptation is not a problem.

30

RELATIVE WATER CONTENT, XYLEM PRESSURE POTENTIAL, AND TRANSPIRATION RATE IN RELATION TO DROUGHT RESISTANCE IN SIX DESERT SHRUBS OF NORTHWEST CHINA. Z.Q.Wang, J.B.Zaerr, Oregon State University, Corvallis, Y.C.Cai, X.Liu, Ningxia Forest Research Institute, Yinchuan, P.R.China.

This study examines some of the physiological characteristics of six desert shrubs indigenous to an arid region and growing in Ningxia, northwest China. Caragana korshinskii and C.intermedia tolerated water stress at lower Ψ_p and were able to adjust relative water content and transpiration rates both daily and seasonally when stress became severe. Zygophyllum xanthoxylum and Nitraria tangutorum depended on well-developed water storage organs in their leaves and on reduced transpiration rates. Hydysarum scoparium and H. fruticosum have large root systems to absorb water from different soil layers, and their Ψ_p was generally higher than that for the other species. The results indicate that the desert shrubs have different mechanisms for tolerating the water deficit.

31

MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF DOUGLAS-FIR, WESTERN LARCH, ENGELMANN SPRUCE, AND LODGEPOLE PINE TO CHANGES IN SOIL MOISTURE POTENTIAL AND LIGHT INTENSITY ON A BURNED, MESIC, SOUTH-EXPOSED SITE WITH TWO LEVELS OF VEGETATION REMOVAL. David Crampton and D.P. Lavender.

Seedlings were planted in the spring of 1986 on a prescribed burn of two intensities and an unburned control. In half of the plots established vegetation was removed for three years. Biomass partitioning and measures of stomatal conductance and plant moisture stress were recorded. Fourth year results indicate that the seedlings planted in the unburned control have begun to parallel the growth rates of those planted in the burn. Microenvironmental conditions which were initially favorable for seedling growth in the burn, were also conducive to growth of competing vegetation. Where possible, harvest techniques which leave the humus intact, and remove enough debris to facilitate planting would be more effective in the long term.

32

VISIBLE DAMAGE IN WHITE SPRUCE SEEDLINGS AFTER SHORT DAY LENGTH TREATMENT. S.L. GILLIES & W.E. VIDAVER, Simon Fraser University, Burnaby, B.C.

Short day (SD) length (12 h) was used in July to influence height growth and cold tolerance in white spruce (Picea glauca) seedlings. Container grown 1-0 white spruce seedling controls, 2 week SD (2SD) and 5 week SD (5SD) treatments were assessed two months after SD treatment. Seedlings with moderate and severe visible damage had yellow chlorotic needles, poor root development, lower variable Chl fluorescence and higher thiol levels. Control seedlings had no visible damage, 6% of the 2SD and 35% of the 5SD had moderate to severe visible damage. SD treatment appeared to increase susceptibility to photodamage and contributed to poor root development.

Funding from NSERC of Canada is gratefully acknowledged.

33

ROOT GROWTH IN SPRUCE SEEDLINGS PLANTED AFTER STORAGE: EFFECT OF STORAGE DURATION DEPENDS ON SOIL TEMPERATURE. E.L.Camm and G.Harper. Department of Forest Sciences, University of British Columbia, Vancouver.

Freezer storage of interior spruce seedlings for reforestation is a widely used practice. We examined the effects of storage duration and outplant soil temperature on root number in seedlings during the first month growth following storage. Seedlings were removed from storage at 1 month intervals, and planted in soil at 3, 7 and 11°C (air temp 11°C). After 28 days growth at this temperature, new roots were counted. (i) There can be a transient increase in root growth for this species; the highest number of long (>10mm) roots was produced in 11°C soil after 14 wks storage. (ii) The expression of root growth potential is dependent upon soil temperature; at 3 and 7°C, root number is only 11 to 30% that at 11°C, and the transient increase in number is not seen. (iii) The number of smaller roots (5-10 mm) followed a slightly different pattern. The observed differences in root morphology may be due to storage-related changes in temperature sensitivity of root initiation. Supported by the British Columbia Science Council.

34

PLANT GROWTH PROMOTING RHIZOBACTERIA FOR CONIFERS. C.P. Chanway, University of British Columbia, Vancouver, B.C.

The effect of plant growth promoting rhizobacteria (PGPR) was tested using three conifer species. Inoculation of lodgepole pine (Pinus contorta Dougl.), white spruce (Picea glauca Voss.), and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco seed or seedlings with Bacillus strains promoted seedling emergence and growth in containers or pots. Bacillus strains L5 and L6 significantly increased the rate of white spruce seedling emergence while strain L6 enhanced the number of lodgepole pine seedlings that emerged. These strains also stimulated shoot and root growth of lodgepole pine under sterile or non-sterile growth conditions. Growth of white spruce was unaffected by bacterial inoculation. Root surface area of Douglas-fir was stimulated by inoculation with strain L6. Inoculation of 1-0 containerized lodgepole pine grown in pots in the greenhouse with strain L6 caused a significant increase in shoot biomass. It is concluded that PGPR can enhance conifer growth under controlled environments and that bacterial inoculants may be a valuable tool in silviculture.

35

EFFECTS OF SOIL TEMPERATURE AND MYCORRHIZAL INOCULATION ON WHITE SPRUCE (PICEA GLAUCA) SEEDLING GROWTH AND PHYSIOLOGY. L.D.Husted, Univ. of B.C., Vancouver, B.C.

Cold-stored container-grown white spruce seedlings inoculated as germinants with either E-strain, Hebeloma crustuliniforme, Laccaria bicolor, Thelephora terrestris, forest floor from northern B.C. or autoclaved cultures (control treatment) were transplanted into forest soils maintained at one of two temperatures (5,12 C) representative of northern B.C. planting sites. The objective was to examine the effects of mycorrhizal inoculation on root development, net photosynthesis, water relations (stomatal conductance and resistance to water flow) during the period of transplant shock. Mycorrhizal treatments had significant ($p<0.05$) impacts on both growth and physiological variables; differences between treatments were greatest at the 5 C soil temperature. Treatment means reflected in part the size and foliar nutrition of seedlings at the time of transplanting. Seedling size and nutrient content were influenced ($p<0.01$) by mycorrhizal treatment in the nursery.

36

EFFECTS OF SHORT PHOTOPERIOD TREATMENTS DURING LATE SUMMER UPON THE HARDINESS AND ABSCISIC ACID CONTENT OF BOREAL FOREST SEEDLINGS. D.P. Lavender, S.N. Silim & L. Charleson, University of British Columbia, Vancouver.

Container-grown seedlings of species indigenous to the boreal forests of Canada were grown according to standard British Columbia nursery scenarios until late July. At this time they were subjected to daily eight hour photoperiods for either one or two months. Subsequently, the test populations were evaluated for cold hardiness, abscisic acid content, and outplanted in October in plantations on the University of British Columbia campus and near Williams Lake in the interior of British Columbia. Seedling response varied by species but, generally, the short photoperiod treatment resulted in greater cold hardiness during fall, greater abscisic acid content, and higher field survival.

37

EFFECTS OF A DAILY PHOTOPERIOD DURING COLD STORAGE ON THE PHYSIOLOGY AND GROWTH OF BOREAL FOREST SEEDLINGS. D.P. Lavender, S.N. Silim, & L. Charleson, University of British Columbia, Vancouver.

Container-grown seedlings of species indigenous to the boreal forests of Canada were grown according to standard British Columbia nursery scenarios until early February, when they were placed in cold (ca 1° C.) storage with and without a daily 12 photoperiod. Populations of each species were outplanted in March and May in plantations on the University of British Columbia campus and near Williams Lake in interior British Columbia. In addition, white spruce (*Picea glauca* (Moench.) Voss). and lodgepole pine (*Pinus contorta* Dougl.) seedlings were grown for five weeks in controlled environment facilities. The seedling response varied with species, but in general the daily photoperiod treatment resulted in a more rapid shoot growth initiation and slightly increased root growth.

38

PATTERNS OF COLD HARDENING AND DEHARDENING OF WHITE SPRUCE (*PICEA GLAUCA* (MOENCH.) VOSS) SEEDLINGS. S.N. Silim, D.P. Lavender and L. Charleson, University of British Columbia, Vancouver.

Container-grown white spruce seedlings were exposed to moisture stress, moderate and low temperatures and long and short photoperiods in various combinations and then evaluated for development of cold hardiness. In general, the short photoperiods stimulated greater hardiness than moisture stress and the combination short photoperiod-moderate temperature followed by low temperatures gave the greatest hardiness. Dehardening was strongly affected by degree of chilling seedlings had received with incompletely chilled plants dehardening very slowly, completely chilled, rapidly when exposed to warm temperatures.

39

ENVIRONMENTAL CONTROL OF FROST HARDINESS IN SEEDLINGS OF WESTERN RED CEDAR (*THUJA PLICATA* D. DON) AND YELLOW CEDAR (*CHAMAECYPARIS NOOTKATENSIS* (LAMB.) SPACH.). S.N. Silim, L. Charleson, & D.P. Lavender, University of British Columbia, Vancouver.

Effects of photoperiod and water stress followed by low temperatures on frost hardiness of container-grown cedars were examined.

Photoperiod had no effect on the development of frost hardiness of red cedar and moisture stress, only a minimal effect. Exposure to temperatures just above freezing resulted in an increase hardening of ca 3° C. per week. Sub-freezing temperatures (-3° C. produced a higher rate of hardening (ca 10° C. per week). Yellow cedar seedlings responded to both photoperiod and moisture stress treatments with a slight increase in cold hardiness. The effect of low temperatures was similar to that of red cedar.

40

EFFECTS OF SEVERAL SITE PREPARATION TECHNIQUES UPON THE SHOOT AND ROOT GROWTH OF WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) VOSS.) AND LODGEPOLE PINE (*PINUS CONTORTA* DOUGL.) SEEDLINGS. D.P. Lavender and L. Charleson, University of British Columbia, Vancouver.

Container grown white spruce and lodgepole pine seedlings were outplanted in six areas in north central British Columbia after a series of site preparation treatments which included the use of plows, mounders, patch scarifiers, and disc trenchers. Seedlings were harvested three times during the growing season following planting and at the end of each of the two following years and the shoot and root growth evaluated. Generally, the greatest growth was made by seedlings planted on raised microsites, although root elongation of many seedlings was very limited.

41

DNA FINGERPRINTING IN STUDIES OF NATURAL POPULATIONS. S. A. Cummings and J. G. Hallett, Washington State University, Pullman.

DNA fingerprinting promises to be a powerful tool for exploring previously unapproachable questions on the ecology of natural populations by revealing the familial relationships and reproductive contributions of individuals. We examined the utility of two DNA probes in such studies: a minisatellite repeat isolated from a house mouse genomic library and a short repetitive CAC segment. DNA samples from several field voles (Microtus montanus) were cut with restriction enzymes, separated on agarose gels , and blotted to nylon membranes. A non-radioactively labeled (digoxigenin) oligonucleotide probe was hybridized to each membrane and the "fingerprint" pattern was created directly on the membrane by an enzymatic color reaction. Both probes revealed variations in the banding patterns of individuals. The CAC probe provided a greater number of resolvable bands (18-20) than did the mouse minisatellite (5-7) and showed high variation between individuals. The CAC probe should prove useful in field investigations.

42

A COHORT MODEL OF MICROTINE RODENT DYNAMICS. J. G. Hallett and M. A. O'Connell, Washington State University, Pullman.

Negus et al. (1986) suggest that fluctuations in abundance of microtine rodents might be understood by examining the differences between cohorts within a population. They found that population densities of Microtus montanus were remarkably stable within a homogeneous habitat undergoing similar yearly patterns of environmental change. At a site where the time of seasonal changes varied, populations showed greater fluctuations. In this paper we examine the validity of the argument put forward by Negus et al. (1986) by constructing a simulation model that follows the production of separate cohorts throughout the year. The initial model mimicked the predictable environmental conditions described in Negus et al. (1986) for Microtus montanus and resulted in annual cycles. Greater temporal heterogeneity was added by varying season length and production or by changing survivorship patterns. Either component increases the variance in population numbers between years. The results support suggestions that seasonality is a major contributor to population fluctuations.

43

EVALUATION OF THE REPELLENCY OF POWDERED STARLING TO DEER AND MOUNTAIN BEAVERS. **D. L. Campbell and J. P. Farley, USDA APHIS S&T, OLYMPIA, WA.**

Starling (Sturnus vulgaris) carcasses taken in damage control operations were processed into a powder and tested on 2-year-old Douglas-fir (Pseudotsuga menziesii) seedlings to reduce damage by penned black-tailed deer (Odocoileus hemionus columbianus) and free-roaming mountain beavers (Aplodontia rufa). Seedlings were sprayed with Rhoplex AC-33 adhesive (10% or 23% solids) and dusted with 2 or 3 g powdered starling (PS). After a 2-month exposure to dormant seedlings, deer browsed none of the PS treatment, 50% of the Rhoplex-only treatment, and 66% of the controls (n=130). After a 2-month exposure to treated growing seedlings, deer browsed 8% of the PS seedlings, 89% of the Rhoplex-only treatment, and 83% of the controls. Mountain beavers cut 13% of dormant PS seedlings when PS-treated cull seedlings were placed in burrows, 30% of PS seedlings when no culls were in burrows, and 81% of controls (n=144) after 2 months; damage to both PS treatments had increased to 54% and damage to controls was 96% after nearly 12 months. Powdered starling is a good candidate short-term repellent for deer and mountain beavers.

44

TERRESTRIAL VERTEBRATE ABUNDANCES IN RED ALDER (ALNUS RUBRA) FORESTS IN THE OREGON COAST RANGE. **C. Chambers, Oregon State Univ., Corvallis, W. McComb, Oregon State Univ., Corvallis, M. Newton, Oregon State Univ., Corvallis.**

Small mammal and amphibian community structure and diversity were characterized for 40 to 50 year old red alder stands on three sites in the Oregon Coast Range. Thirty-four species were live-captured during dry and wet fall seasons. The most abundant species were deer mice, Trowbridge shrews, roughskin newts, Pacific shrews, Ensatina salamanders, and Townsend chipmunks, representing 85% of all captures. Total captures of amphibians were higher during the wet fall season (30%) than dry fall (5%). Community similarity within and between sites was consistently high, averaging 78% and 77%, respectively. Simpson diversity indices averaged 75% for all sites. Simpson equitability averaged 79%. Habitat features, such as logs, stumps, shrub cover, and proximity to streams were important to some species in these alder stands.

45

RESULTS OF TWO YEARS OF SPOTTED OWL INVENTORIES IN THE UPPER SKAGIT RIVER DRAINAGE. W.L. Gaines, E.R. Garcia, J.L. Bush, and A. Sprague. U.S. Forest Service, Winthrop, Wa.

We inventoried for spotted owls (Strix occidentalis caurina) in the remote upper Skagit River drainage during 1988 and 1989. We inventoried an average of 300 miles (one way) of roads, trails and cross-country routes discovering 5 and 7 adult spotted owls during the 1988 and 1989 field seasons, respectively. We discovered 1 pair and 3 individual adults in 1988, and 3 pairs and 1 individual in 1989. During the 2 full seasons of inventory, only 1 pair was suspected to be reproductive. Spotted owls occupied forests containing many large snags, a high degree of dead and down debris, multi-layered canopies, and very large trees.

46

LITTER SPIDERS OF THE WESTERN CASCADES: SUCCESSION AFTER CLEARCUTTING. J.D. McIver, A.R. Moldenke, G. L. Parsons. Entomology, OSU, Corvallis.

Seasonal samples from a matrix of 4 successional stages (clearcut to oldgrowth) by 8 moisture regimes (varying in slope/aspect) of Pacific Northwest conifer forest were examined relative to leaf litter spider fauna. Multivariate analysis of the 35 most common species indicated successional stage to be the primary determinant of community structure with patterns of species composition also influenced by moisture and season. The oldgrowth spider fauna, dominated by native trapdoor spiders and microweb spinners, is replaced after clearcutting by a suite of diurnal pursuit hunters and nocturnal ambush hunters characteristic of disturbed, open areas. In 30 years after clearcutting, the wettest sites regain most of their original fauna, but the driest sites still exhibit much of the typical clearcut species composition.

47

CONVERTING SOLAR POWERED CALCULATORS TO DATA LOGGERS. L.R. Askham, Washington State University, Pullman.

The expense of collecting large amounts of data at remote field sites over an extended period of time can be expensive and time consuming. For many researchers the cost of purchasing electronic data loggers to record activity events has, until now, been prohibitive. Faced with the same situation, solar powered calculators were converted to record the diurnal and nocturnal activities of raptors during an extensive field study. The results are that when combined with systematic observations the device can now be used to collect large amounts of data with high levels of accuracy for only a few dollars.

48

ENVIRONMENTAL IMPACTS AND SOCIAL CONFLICT CAUSED BY OFF ROAD VEHICLE USE IN THE ROSLYN-CLE ELUM AREA OF WASHINGTON STATE. Eric C. Phillips, Central Washington University., Ellensburg.

Off road vehicle use in the Roslyn-Cle Elum area is virtually unmanaged, and occurs on both private and public lands. A full season (summer) was spent interviewing users and community members as well as making observations. Problems include noise, private property damage, environmental effects, and community conflict. Alternatives available to the major local land managers and recomendations to resolve the conflict will be given.

49

MODELING REGIONAL RECREATION PATTERNS: TOWARD COMPREHENSIVE RECREATION RESOURCE PLANNING IN THE NORTHWEST. D.C. Hospodarsky, Oregon State Univ., Corvallis.

One informational requisit for cooperative recreation planning among public land management agencies is a regional estimate of future recreation activity consumption from which to devlop plans. The objective ofthis study was to model the outdoor recreation behavior of Oregon, Washington and Idaho residents through 2010 by estimating consumption of 60 activities within 18 zones comprising the states. Baseline consumption levels were estimated from yearlong surveys in each state. 7307 adults completed telephone interviews and were sent mail questionnaires; 68 percent were returned. Projections of future consumption were made using U.S. Forest Service national models with county-level recreation demand/supply data as regression parameters. Activitys' growth potentials are described and zones classified as recreation experience importers or exporters. Implications to agencies are discussed.

50

REGIONAL SIGNIFICANCE OF THE DRYDEN RHYTHMITES AND DROPSTONES, WENATCHEE RIVER VALLEY, WASHINGTON. W.A. Long, 123 Riverfront Dr., Cashmere, WA 98815

Before Okanogan-lobe blockage, at least one Lake Missoula flood as deep as 350 m descended the Columbia River valley, carried ice-rafted erratics to altitude 485 m in the Entiat-Vantage valley segment, and surged 25 km up the Wenatchee River valley. Rhythmites at Dryden contain a graded fine sand-silt bed 60-75 cm thick for each of 7 or more Lake Missoula floods. The Dryden rhythmites have no apparent upward thinning and contain unweathered granitic dropstones from up-Columbia provenance. Morainal and erratic-boulder correlations indicate the possibility that the Chelan glacier was a source for many Wenatchee valley erratics. Granodiorite boulders transported from the Stuart Range ice rafted from upvalley and embedded in the sand-silt body near Peshastin indicate flood surges occurred when the Icicle Creek glacier was at its maximum Leavenworth stand. With maximum ponding behind the Wallula Gap dam at 350 m, only a Lake Missoula flood down an unobstructed Columbia Valley could have surged up the Wenatchee to altitude 450 m.

51

BEDROCK AS A SOURCE OF WATER FOR SCLEROPHYLL VEGETATION. M. Newton and Zhengqi Wang, Oregon State University, Corvallis

Stands of Arbutus menziesii and Arctostaphyllos viscida depleted water in bedrock long after surface soil was depleted. The metasedimentary rocks stored water much like soil, but at densities of 2.1-2.3. Root penetration by manzanita and madrone is 3.5 m or more, and rocks at 1.5 m release 2.1 to 12.7 percent water during the summer rain-free season. Total water content of rocks at "field capacity" ranges from 13 to 21 percent. This large water reservoir is an important source of dry-season transpiration, and probably supplies most of the water used in mid-summer primary production. Extraction of water from bedrock creates a storage opportunity capable of absorbing intense rains. It is also a crucial zone in competitive interactions among woody species.

52

A PRACTICAL ASSESSMENT OF THE WETLAND EVALUATION TECHNIQUE (WET) AS A TOOL FOR MEETING OREGON'S LAND USE PLANNING GOAL FIVE REQUIREMENTS. J.A. Griffith and P.L. Jackson, Oregon State Univ., Corvallis.

This paper discusses the use of the Wetland Evaluation Technique (WET) as a practical, rapid assessment methodology for meeting the policy directives set forth in Oregon's LCDC Goal 5 concerning natural area inventory and analysis. The issue of practicality was addressed from the standpoint of time, manpower, and the relative value of the results obtained from its use. A case study evaluated the Jackson-Frazier Wetland near Corvallis and concluded that WET produces wetland significance values comparable to other methodologies requiring greater time and expertise. However, to take the evaluation beyond the first level ratings requires significant time and expertise. This situation could pose considerable practical difficulties for those county land use planning agencies with large numbers of wetlands within their jurisdictions.

53

COMPARISON OF PRESETTLEMENT AND PRESENT OLD-GROWTH FOREST COMMUNITIES IN THE SHAWNEE HILLS, ILLINOIS. Fred B. Crooks, Oregon State University, Corvallis.

Witness tree data from the 1806-7 original land survey records were used to reconstruct forest community landscape patterns in the Shawnee Hills of southern Illinois. Section and quarter section corners were located on topographic maps and categorized by site-type: alluvial, low north slopes, high north slopes, ridgetop and south slopes. Quercus alba was found to be the most important species on all site-types in the presettlement forest. Sugar Maple (Acer saccharum), which presently dominates old-growth stands on mesic alluvial and low north sites, was considerably less important in the presettlement forest. Across comparable sites, the community composition pattern in the presettlement forest appeared to be more similar to that of disturbed second-growth forest than to undisturbed old-growth forest found in the Shawnee Hills.

54

IMAGE BASED SOIL FAUNA TAXONOMY USING HYPERCARD ON A MACINTOSH COMPUTER C.H. Shaw, A. Moldenke and J. R. Boyle. Oregon State University. Corvallis

Many individuals are interested in the contribution fauna make to the soil processes they study. Interest often wanes once they are faced with the investment in time and effort required to obtain the taxonomic skills necessary to expand their research programs to include soil fauna. Learning taxonomy is often viewed as an insurmountable task because;

1) information is not in single source
2)traditional keys are limited to verbal descriptions to teach a visual skill
3) dichotomous keys are tedious and require detailed knowledge of body structures.

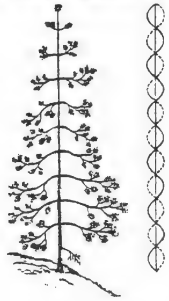
We have developed a taxonomic key for soil invertebrates using Hypercard on the Macintosh computer. Advantage of our key include;

1) image based and requires minimal previous knowledge of body structures
2) present multiple rather than tedious dichotomous choices
3) open ended and can be rapidly updated
4) duplication is rapid and inexpensive
5) ideal for classroom instruction
6) immediately useful to the novice
7) instant access to ecological literature
8) provides experienced user with a detailed database storage and retrieval system
9) provides the capability to identify to the species level when desired.

55

INTERACTION OF W-WAVES AND GRAVITY. Q.E. Wagner. Wagner Research Lab., Rogue River, OR 97537.

Gravity may organize W-waves with standing W-waves tending to move along gravitational field lines (see Figure). In turn W-waves may modify gravity. Confirming this are the following: (1) 80Hz signals from vertically displaced W-wave sources were related by a constant phase (sufficient to prove the hypothesis but more data is needed). (2) Plant gravitropism (the usually accepted theory is questionable). (3) The observation of weight changes in vertical holes in tree xylem seem to indicate that W-waves interact with gravity. (4) The so called "fifth force" measurements.



56

THE EFFECT OF TEMPERATURE, MOISTURE AND SOIL ACIDITY ON LIGNIN AND CELLULOSE DECOMPOSITION IN FOREST SOILS. J.A. Entry, P.K. Donnelly, D.L. Crawford, K. Cromack, Jr., Oregon State Univ., Corvallis and U. of Idaho, Moscow.

Cellulose and lignin are two abundant organic substances present in forest floors. Microbial biomass, lignin and cellulose decomposition rates were measured for six weeks in forest soil microcosms and with pHs of 4.5, 5.5 and 6.5 adjusted to 20, 40 or 60% moisture content at temperatures of 4, 12 and 24•C. Lignin and cellulose decomposition rates significantly increased at higher soil temperatures and moisture contents. Microbial biomass was greater at higher soil moisture contents. Microbial biomass, lignin and cellulose decomposition were not affected by soil acidity. Soil moisture was more important in affecting microbial biomass than either soil temperature or soil acidity.

57

DISTRIBUTION OF NUTRIENTS AND TRACE METALS IN THE PROFILES OF SOILS AMENDED WITH MUNICIPAL SEWAGE SLUDGE AFTER 15 YEARS. Dongsen Xue, Rob Harrison and Charles L. Henry, University of Wasington, Seattle.

Application of municipal sewage sludge into forest environments typically results in significant increases in trace metals in surface soil horizons in the short term. Concern that long-term leaching of certain trace metals through the profile of coarse-textured soils might result in contamination of groundwater persists, since definitive studies of sludge application on extremely coarse textured forest soils are scarce. This study anlayzed trace metal concentrations in coarse glacial outwash forest soils fertilized 15 y previously with 500 Mg/ha of municipal sewage sludge. After 15 years the soil profile to a depth of 2 m was sampled and pH, CEC, C, N, P, Cd, Cu, Ni, Pb and Zn were quanitified and compared to an adjacent control soil. Total C, N, P, CEC, Cd, Cu, Ni, Pb and Zn values were significantly higher in surface horizons (0-17cm) of sludged compared to the control soil. Soil pH was lower in the sludged vs control soils. Migration of all constituents except Pb and Cu into the subsoil (17-27 cm) was noted to a small degree. With the possible exception of Ni, no sludge constituents measured leached to the maximum depth of 2m.

58

WATER QUALITY OF GLACIAL AND NON-GLACIAL STREAMS IN MOUNT RAINIER NATIONAL PARK. G.L. Larson, National Park Service, Oregon State University, Corvallis; C. Hawkins, Olympic National Park, Port Angeles; B. Samora, Mount Rainier National Park, Tahoma Woods; and S. Gibbons, Mount Rainier National Park, Tahoma Woods.

Glacial and non-glacial streams were, in general, slightly basic and low in conductivity, alkalinity, nitrogen, phosphorus and cations. Most glacial streams were turbid with glacial flour, especially in summer, but some were nearly as clear as non-glacial streams. Water temperatures were low at sampling sites near glaciers throughout the year. Water temperatures increased downstream, and beyond 10 km all streams were at about the same temperature for a given season. Maximum mean summer water temperatures at the most downstream sites ranged between 8 and 12°C. In summer, glacially fed sites tended to be highest in phosphorus, while sites with little or no glacial influences were highest in Kjeldahl-N, ammonia-N, and alkalinity. Water quality was influenced by geologic formations, glacier area, time-of-day, season, sample location along elevational gradients, and input from mineral springs.

59

TEMPORARY STREAM COMMUNITIES IN WESTERN OREGON: LIFE HISTORIES OF DOMINANT MAYFLIES AND STONEFLIES. M. DIETERICH AND N.H.ANDERSON, OREGON STATE UNIVERSITY, CORVALLIS.

Colonisation substrates (leaf packs and sediment baskets) and emergence traps were used to study invertebrate communities in temporary streams in McDonald Forest near Corvallis, OR.

Paraleptophlebia gregalis, Ameletus similor, Ostrocerca foersteri, Soyedina interrupta, Sweltsa fidelis and Calliperla luctuosa were the common mayflies and stoneflies in streams drying up in early summer. In channels ceasing flow as early as April, only P. gregalis was abundant; 3000 subimagos emerged from a seep of ca. 0.3 m in 1988.

All taxa except O. foersteri showed facultative strategies for drought survival in that eggs as well as larvae could survive the dry season. Early instar larvae were found in seep areas during the summer and within the first month after resumption of flow in late fall.

It is concluded that temporary streams can provide important habitat for presumably rare aquatic insects and therefore need to be considered in plans for watershed management.

60

REARING ECOLOGY OF JUVENILE STEELHEAD (ONCORHYNCHUS MYKISS), AND HABITAT ANALYSIS OF STEAMBOAT CREEK BASIN, OREGON. J.M. Dambacher. Oregon State University, Corvallis.

Distribution and abundance of juvenile steelhead (Oncorhynchus mykiss) and other fishes are described from fish population and habitat inventories of 1987 and 1988. The effects of basin scale, water temperature, and habitat quality appear to influence the abundance and habitat utilization of juvenile steelhead. The distribution and abundance of redside shiner (Richardsonius balteatus) appear to be strongly influenced by water temperature, and their habitat utilization by the presence of steelhead. Fish trapping during the spring of 1988 revealed that roughly 25,000 age 1+ steelhead migrated out of the basin compared to only 1,500 smolts. This life history pattern is discussed in the context of habitat quality and a basin perspective.

61

TRACKING THE LIMNOLOGICAL RECOVERY OF VOLCANICALLY IMPACTED SPIRIT LAKE, MT.ST. HELENS, WASHINGTON: 1980-1989. D.W. LARSON, CORPS OF ENGINEERS, PORTLAND, OR.

The limnological recovery of Spirit Lake, WA was tracked for several years beginning in 1980 when the lake was altered substantially by the volcanic eruption of Mt.St.Helens. Shortly after the eruption, the lake's phytoplankton community consisted of only a few diatom species, whose total density was 260 cells/ml. Since 1980, species diversity and densities have increased markedly. Between 1983 and 1989 we identified 120 species and measured biomass and ppn. C-14 uptake experiments indicated that the production of organic matter in the lake, all chemosynthetically derived in the period 1980-81, is now carried on photosynthetically by lake phytoplankton. This paper also discusses other post-eruption limnological changes that are indicative of lake recovery.

62

STATUS OF FISH POPULATIONS AND MANAGEMENT OF MOUNTAIN LAKES IN THE WESTERN U.S. P.F.Bahls,Oregon State Univ.,Corvallis.

To determine the status of fish populations and management of mountain lakes in the West, state fishery managers in each of 40 regions in 11 states were interviewed. Of about 14,000 mountain lakes in the West, managers estimate that less than 5% contained trout prior to stocking. Presently, about 60% contain trout and 80% of these are regularly stocked, although more than 50% may have wild (self-sustaining) populations. Less than 5% of the deeper(>3 m),larger (>2 ha) lakes remain without fish. Most regions manage mountain lake fisheries with limited or no survey or research data on which to base intensive stocking programs and limited consideration of potential effects of stocking on indigenous trout, other aquatic species, or lake ecosystems. Regions are detailed that expanded surveys and reduced stocking to protect and enhance native and wild trout and pristine fishless lakes.

63

EFFECTS OF STOCKED TROUT IN NATURALLY FISHLESS HIGH MOUNTAIN LAKES OF NORTH CASCADES NATIONAL PARK, WASHINGTON. G.A. Lomnicky, Oregon State Univ., Corvallis.

Aquatic communities including amphibians, zooplankton, benthic macroinvertebrates, phytoplankton, and fish are being field researched from 1989-1991. A classification system has been developed to select lakes for the research. Sixty-five lakes of varying surface area, basin geology, depth, watershed vegetation, aspect, and elevation were sampled during the 1989 summer field season to provide a broad base of information from lakes of varying classes. The 1990 field season will involve intensely studying a selected subset of these lakes that are of the same class, some with fish and others without fish. Initial results suggest native aquatic communities and water quality differ in various lake classes.

64

PROPAGULE SOURCES OF REVEGETATION AFTER DISTURBANCE. D.L. Clark and M.V. Wilson. Oregon State Univ., Corvallis.

We investigated propagule sources of revegetation following logging and burning of an old growth Douglas-fir forest. In general, old growth species established from vegetative propagules only. Old growth species were poorly represented in both the old growth seed bank (53 seeds/m^2) and the disturbed seed bank (11 seeds/m^2). However, 76% of the pre-disturbance species were capable of sprouting after fire. Vegetative propagules of these species contributed 69% of the individuals establishing in the field plots the first year, while 31% established from seed. The establishment rate in the second year was 1600% that of the first year. Only 2% of the second-year establishment was from vegetative propagules; 98% from seed, primarily on-site dispersed seed. Of the 32 taxa involved in revegetation only 9 species established in both years. These results show the importance of the relative contribution of propagule sources in determining species composition and abundance of revegetation immediately after disturbance.

65

SEED BANKS OF FOUR MICROHABITATS IN ALPINE TUNDRA OF THE OREGON HIGH CASCADES. C.A. Ingersoll and M.V. Wilson, Oregon State Univ., Corvallis.

The size and floristic composition of the persistent buried seed bank was assessed in soils collected from four microhabitat types in alpine tundra. Overall density was 3435 seeds/m^2. The seed bank was heavily dominated (75%) by Juncus drummondii, which is present but not abundant in the aboveground vegetation. Two dominant species, Saxifraga tolmiei and Carex nigricans, each contributed another 10% of the buried seeds. All other species abundant in the vegetation were absent or rare in the seed bank. Seed bank densities ranged from 1400/m^2 in the nonvegetated microhabitat to 8800/m^2 in moss mats. Intermediate densities were found in and around vascular plants. The many buried seeds even on barren sites suggests that the low vegetation cover of this community is not due to a lack of seeds.

66

SEED DORMANCY IN ALPINE-SUBALPINE PLANTS. T.N. Kaye, Oregon State Univ., Corvallis.

Seed germination is a crucial event in the life of every sexually reproduced higher plant. A portion of the seeds of many species are dormant; they do not germinate unless certain conditions are met. The objective of this research was to determine the extent of seed dormancy in 28 species of grasses and forbs from alpine-subalpine areas of the Olympic Mountains, Clallam Co., Washington. Five species were non-dormant. After-ripening improved germination of eight species, five required prechilling, scarification benefited four, and some seeds of 11 species required light. Four others failed to germinate at all. At least one species possessed more than one dormancy mechanism. Seed dormancy may control germination timing and rate, which in turn effect plant establishment and competitive ability, and ultimately population, succession, and community patterns of high-elevation vegetation. Knowledge of germination characteristics improves propagation success and aids efforts to revegetate disturbed areas in Olympic National Park.

67

GERMINATION OF WHITETOP (CARDARIA DRABA L.) and diffuse knapweed (CENTAUREA DIFFUSA LAM.) AS INFLUENCED BY OSMOTIC AND SALT STRESSES. G. Kiemnec and L. Larson, Oregon State Univ., Corvallis.

The spread of weeds in rangelands can be limited by specific water requirements or salt tolerance. A growth chamber study was initiated to determine the seed germination response of two weed species, whitetop and diffuse knapweed, to osmotic and salt stresses. Seeds experienced osmotic stress from exposure to polyethylene glycol (PEG) solutions (0, 0.5, 1.0, and 1.5 MPa) and salt stress from exposure to NaCl+CaCl2 solutions (0, 4, 8, and 12 dS/m). Increasing PEG concentrations reduced total percent germination and delayed initial germination of whitetop. Total percent germination for knapweed was highest at 0.5 MPa of osmotic stress. Increasing PEG concentrations delayed knapweed germination. No germination occurred at 1.5 MPa of osmotic stress for either species. Percent germination of whitetop was slightly lowered by salt stress at 12 dS/m as compared to 0, 4, or 8 dS/m. Percent germination of knapweed was decreased by salt stress, but no trend was apparent.

68

FIRST-YEAR DEFOLIATION EFFECTS ON WHITETOP *(Cardaria draba (L.) Desv.)*. M.L. McInnis, L.L. Larson, R.F. Miller, Dept. Rangeland Resources, Oregon State Univ., Corvallis.

A study was established near Baker, Oregon to determine the effects of defoliating whitetop during 3 phenological stages: bolting, early flowering, and full flowering. The experimental design was a randomized block with 5 blocks per treatment, each 3 x 12 m in size. Defoliation was accomplished using a gas-powered string clipper to clip all plants within each block at ground level. Measurements taken at the end of the growing season indicated regrowth of clipped plants was less tall, produced less above-ground biomass, fewer vegetative and reproductive stems, fewer seeds, less heavy seeds, and lower seed viability than control plants. Phenology of subsequent regrowth of defoliated plants was more uniform at any given date than that of the control. Plants clipped during full flowering were less tall and had lower seed viability than plants clipped earlier in the season. While defoliation alone is not expected to be an effective long-term control of this weed, properly-timed grazing followed by herbicide application may increase mortality.

69

VEGETATION AND FLORA OF MYRTLE ISLAND RESEARCH NATURAL AREA, OREGON. R. L. Thompson, Berea College, Berea, Kentucky.

Myrtle Island Research Natural Area was established to preserve an old-growth Umbellularia californica and Pseudotsuga menziesii stand on an 11.3 ha. island in the Umpqua River Valley of the Coast Range in 1951. The island is an excellent example of a hardwood forest within the Interior Valley (Pinus-Quercus-Pseudotsuga) Zone of western Oregon. Twenty (15m x 25m) plots were used to obtain forest structure, understory vegetation, and floristic composition. Four community types are described from canopy coverage and frequency of the dominant trees, shrubs, and herbs: Salix/Equisetum, Alnus/Rubus/Phalaris, Quercus/Cytisus/Agrostis, and Umbellularia-Pseudotsuga/Acer/Polystichum. The flora consists of 77 families, 226 genera, and 345 specific and infraspecific taxa. Of these species, 137 (40 %) are naturalized. The Poaceae (43), Asteraceae (42), Fabaceae (24), Rosaceae (16), Cyperaceae (16), Brassicaceae (14), Caryophyllaceae (13), Scrophulariaceae (13), and Lamiaceae (12) comprise 56 % of the total taxa. The species richness within the plant communities of the riparian habitats on Myrtle Island is a function of the fluvial seed banks and alluvium from the Umpqua River, climate, physiography, and existing vegetation.

70

RARE PLANT SURVEYS FOR THE KOMA KULSHAN HYDROELECTRIC PROJECT, MOUNT BAKER, WASHINGTON. Clayton Antieau and Colleen McShane, Ebasco Environmental, 10900 NE 8th St., Bellevue, Washington 98004-4405.

A rare plant survey conducted during June and July, 1989, on the Sulphur Creek lava flow, Mount Baker, Washington, identified populations of two species currently listed as Sensitive in Washington by the Washington Natural Heritage Program: the tree-like clubmoss (*Lycopodium dendroideum*) and the long-styled sedge (*Carex stylosa*). It was determined that 2,241 stems of tree-like clubmoss and 40.36 square meters of long-styled sedge would be impacted by construction of the Koma Kulshan Hydroelectric Project. Realignment of portions of the project access road and diversion routes reduced the final impacts to 662 stems of clubmoss and to 3.7 square meters of sedge. Because of the location of additional patches of these two species outside the project area, project impacts were below the maximum allowable impact criterion set by the U.S. Forest Service. This is the first case of rare plant species affecting the implementation of any disruptive activity (such as hydroelectric development or logging) on the Mount Baker Ranger District, Mount Baker/Snoqualmie National Forest. This case study emphasizes the needs for: 1) agency preparedness in dealing with rare plant conservation issues, and 2) population ecology data for rare plant species.

71

LIFE HISTORY, POPULATION DYNAMICS, AND CONSERVATION STATUS OF CALOCHORTUS NITIDUS (LILIACEAE). S.L. Caicco, P.O. Box 3823, Lacey, WA 98503.

Calochortus nitidus, a Palouse region endemic, is a Federal Candidate species and U.S. Forest Service Sensitive Species. Although it has been extirpated from 90% of its pre-settlement range, numerous populations still occur on the Nez Perce National Forest in western Idaho. Permanent plots were placed within selected populations in 1988. Two consecutive years of data collection within these plots have provided information on the life history and population dynamics of the species. This annual monitoring has also identified current threats to the reproductive success of the species. These include seed predation by insects, leaf herbivory by small mammals, and the removal of reproductive structures by domestic livestock. The relative impact of these factors increases in the order listed.

72

THE PRESENCE OF *BRACHYPODIUM SYLVATICUM* IN MACDONALD-DUNN FOREST. D.M. Leavell and C.J. Hubbard. Oregon State University, Corvallis.

Brachypodium sylvaticum (Huds.) Beauv. was observed during the summer of 1989 while installing vegetation plots in Oregon State's research forest--the MacDonald Dunn. 115 intensive plots were taken throughout the 14,000 acre forest covering as much of the vegetative diversity as possible. Plots included environmental data such as: slope, aspect, and elevation, as well as vegetation cover percent. Historically, vegetation sampling mentioned *Brachypodium sylvaticum* in limited areas--with a first documented appearance in 1984. During the 1989 survey, *Brachypodium sylvaticum* was found to have increased in area dramatically in comparison to past surveys. The authors found the grass most frequently between 700 and 900 feet in elevation, southeasterly aspects, 20 to 30 degree slopes, and on shallow soils.

73

SOMATIC EMBRYOGENESIS FROM IMMATURE EMBRYOS IN MEADOWFOAM (LIMNANTHES ALBA). D. Southworth and S. Kwiatkowski, Southern Oregon State College, Ashland.

Developing embryos from immature seeds were excised and cultured. Optimal proliferation of differentiated secondary embryos occurred on Murashige-Skoog media containing 7% sucrose, 0.1 µM 2,4-D, and 0.1-1.0 µM zeatin. Higher levels of auxins inhibited embryo proliferation. Secondary embryos were subcultured to produce more embryos. The results indicate the feasibility of clonal propagation of meadowfoam and its suitability for tissue culture.

74

MITOCHONDRIAL RESPIRATION IN GREEN ALGAE
H.G. Weger[1], R.D. Guy[1] & D.H. Turpin[2], [1]Dept. of Forest Sciences, Univ. of British Columbia, Vancouver BC, V6T 1W5, [2]Dept. of Biology, Queen's University, Kingston ON, K7L 3N6

Inhibitor titration curves and discrimination against $^{18}O_2$ by mitochondrial respiration in three strains of green algae were determined. Discrimination for cytochrome pathway respiration ranged from 19.89 to 20.43‰. Discrimination for alternative pathway respiration by wild type Chlamydomonas reinhardtii was 25.46‰, while discrimination values for a cytochrome oxidase-deficient mutant of C.reinhardtii ranged from 24.24 to 24.96‰. NH_4^+ assimilation by N-limited cells resulted in a stimulation of mitochondrial O_2 consumption, in both light and dark. This stimulation was mediated entirely via the cytochrome pathway in wild type C. reinhardtii, despite a large capacity for alternative pathway activity. In the mutant strain, and in wild type cells in the presence of KCN, NH_4^+ assimilation resulted in a stimulation of alternative pathway activity. This suggests that the alternative pathway can function to maintain TCA cycle carbon flow during NH_4^+ assimilation if cytochrome pathway function is compromised.

75

PROTEINS UNIQUE TO CELLULAR DESICCATION IN TISSUES OF CONIFERS. N.C. Vance. USDA Forest Service, PNW Research Station, FSL, Corvallis, OR.

Proteins are synthesized in drought stressed needles of Pinus ponderosa seedlings. Several appear to be specifically related to dehydration. The proteins were detected by polyacrylamide gel electrophoresis, staining and fluorography. Further analysis of pollen and embryos of Pseudotsuga menziesii and P. ponderosa by gel electrophoresis and silver staining reveal proteins specific to a desiccated condition in these tissues. Protection against the effects of severe dehydration is suggested for these proteins.

primary keyword: proteins
secondary keyword: water deficit

76

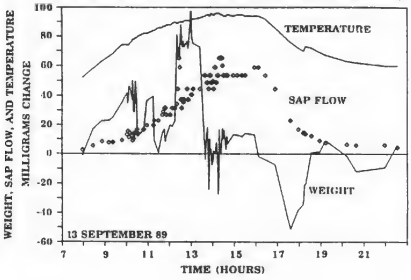
THE EFFECT OF DEFICIENCIES OF N, P, K, AND MG ON PHOTOSYNTHETIC GAS-EXCHANGE PARAMETERS IN LEAVES OF HYBRID 11 POPLAR. R.H. WAGNER. UNIV. OF WASHINGTON, SEATTLE.

Poplar cuttings were grown in a modified gravel culture. N, P, K, and Mg were supplied at three levels: low, medium, and complete (1/2 strength Hoagland's solution). The low level was designed to induce "hidden hunger", a nutrient supply above the appearance of visible symptoms. Plants were grown during winter in a greenhouse under artificial photoperiod and supplemental irradiance. Changes in the partial processes of photosynthesis were inferred from open gas-exchange system measurements. Light-response curves were used to obtain the net photosynthetic rate at light saturation and the photochemical efficiency from the slope at limiting light levels. Dark respiration was measured. Changes in photorespiration were qualitatively estimated from measurements of the CO2-compensation point. Total leaf resistance to CO2-transfer was calculated. Gas-exchange measurements were supplimented by measurements of chlorophyll content and analysis of tissue cations, N, and P.

77

SAP FLOW AND W-WAVES. Q.E. Wagner. Wagner Research Lab., Rogue River, OR 97537.

A mass hanging freely in a small diameter, vertical, sap free hole appeared to gain and lose weight in connection with sap flow. An accelerometer also appeared to confirm the effect. I attribute these effects to an interaction of W-waves with gravity in pumping sap. The interaction would complement root pressure and wicking at times when they are insufficient such as perhaps when plants are dormant or when the sun is not shining as well as provide positive flow in the highest of trees. The following is an example of weight changes observed in madrone (*Arbutus menziesii*):



78

ANNUAL BRANCHING IN THE LICHEN EVERNIA PRUNASTRI IN OREGON. D. F. Stone, 30567 Le Bleu Rd., Eugene, OR 97405 and B. McCune, Oregon State Univ., Corvallis.

Evernia prunastri produces isotomic dichotomous branches at annual intervals in the Willamette Valley of western Oregon, as determined by photographic study and correlations between tree ring counts and lichen thallus branch counts. Branch points can be counted to determine the age of individual thalli. Besides the main dichotomous branches, a variable number of anisotomic adventitious branches are produced from older branches. A small amount of error in age determinations is introduced by occasional irregularities in the branching and previous physical damage to the thallus.

79

LEAD ACCUMULATION IN BRANCH SEGMENTS OF INCREASING AGE IN THE LICHEN EVERNIA PRUNASTRI. B. McCune, Oregon State Univ., Corvallis

Evernia prunastri was collected along a downwind gradient from a point source of lead near St. Helens, Oregon. Thalli were dissected into branch segments of known age and analyzed (AA) separately by age class and site for lead content. The age classes of branch segments spanned the dates of earliest emissions to 2 years after discontinuation of emissions. Average lead contents in whole thalli along the gradient ranged from 921 ppm to 15 ppm as compared to a background rural site near Corvallis, Oregon at 5 ppm. Highest lead contents were in the oldest branch segments (to 11 years old) and secondarily on the branch tips. This pattern appears to be partly the result of superficial particulates. Because branch internodes of E. prunastri appear to continue to thicken and elongate after their first year, reconstruction of a lead deposition chronology from analysis of annual growth segments is complicated by the accumulation of many years of deposition into a single segment.

80

MASS TRANSPLANTS OF ARBOREAL LICHENS. K.A. Enns. Victoria, B.C.

A method for transferring large quantities of Alectoria and Bryoria spp. from old-growth to Douglas-fir juveniles was developed for operational treatments on Vancouver Island. Gelatin adhesives were used. Branches were inoculated (n=2400) with pre-measured dosages of lichen fragments. Pre-, post-treatment and 1st year counts were made. Although ANOVA indicated significant over-all losses, >half the plot means maintained their original number of fragments. Lower elevation plots suffered losses, possibly due to warm summer temperatures. Lichen establishment and growth was evident at upper elevations. Growth and stand manipulation experiments have been ongoing. Transplants of nitrogen-fixing lichens into second-growth is implicated.

81

SAMPLING CANOPY LICHENS W.C.Denison, Oregon State Univ., Corvallis and S.C.Sillett, Univ. of Florida, Gainesville.

The canopy layer of northwest conifer forests supports a rich lichen flora. Sampling lichens of individual trees or stands poses problems of access, quantification and reproducibility. A modified point-intercept method employs a sampling frame for foliated branchlets and a spirally-wound tape for branches. Selected branchlets are removed. Fruticose, foliose, and crustose lichens are sampled. Lichen cover is related to stem surface area. The method is applicable to trees of any age, including old-growth.

82

THE EFFECTS OF AIR POLLUTION ON THE CANOPY LICHEN COMMUNITIES OF OLD-GROWTH DOUGLAS-FIR FORESTS. S. C. Sillett, Reed College, Portland.

The canopies of three old-growth Douglas-fir trees growing within a low elevation forest fragment along the Sandy River were surveyed. Resident lichen communities inhabiting trunks, branches, and twigs throughout the canopy profiles were described both qualitatively and quantitatively, and compared to extant communities inhabiting the canopies of old-growth Douglas-fir trees growing in the H.J. Andrews Experimental Forest, a mid-elevation site in the western Cascades. The canopy lichen communities of the low elevation site were found to be both less species-rich and dominated by pollution-tolerant lichens relative to the mid-elevation site. Nitrogen-fixing lichens, including Lobaria oregana, which dominate the canopies of the mid-elevation site and are thought to play an integral role in old-growth forest nutrient cycles, were conspicuously absent from the canopy communities of the low elevation site. These floristic results are highly suggestive of an air pollution impact on the resident canopy lichen communities of this old-growth forest fragment along the Sandy River, especially considering its close proximity to downtown Portland and an active pulp mill and aluminum plant.

83

A SURVEY OF LICHENS ON QUERCUS GARRYANA IN THE COLUMBIA RIVER GORGE. John R. Davis. Carson Nat'l Fish Hatchery, Carson, WA.

Annual precipitation in the Columbia River Gorge changes from more than 180 cm near Bonneville Dam to less than 40 cm east of Lyle, WA. Lichens on Quercus garryana at elevations of 100-300 feet were examined on the Washington side of the Columbia River from Skamania to east of Lyle. The members of the lichen community change both in relative abundance and species composition. Most of the larger foliose lichens, such as Parmotrema, Platismatia, Pseudocyphellaria, and Sticta, appear to be more abundant at the wetter western end, while Candelaria concolor, Letharia vulpina, and Tuckermannopsis canadensis seem to be more common at the drier eastern end. Some lichens, such as Evernia prunastri, Parmelia sulcata, and Melanelia spp., are present at all sites examined. The rapid change in annual precipitation from west to east in the Columbia River Gorge seems to be the most important factor in determining the species and abundance of lichens present on oak.

84

ASCUS AND SPORE MODIFICATIONS IN EPIPHYTIC HABITATS. M. Sherwood-Pike, Univ. of Oregon, Eugene.

Both lichen-forming and free-living fungi growing on aerial plant surfaces exhibit a high frequency of anomalous ascus structure and unusual spore types, including very large muriform spores, filiform spores, and minute spores in polysporous asci. The spore morphology can be related to the environmental constraints of habitat and it is hypothesized that ascus morphology has become modified in response to the spores.

85

INTERSPECIFIC INTERACTIONS AND SPECIES DISTRIBUTIONS IN THE CORTICOLOUS LICHEN COMMUNITY GROWING ON RED OAKS IN NORTHERN MICHIGAN. E.A. John, Dept. of Botany, University of British Columbia.

Corticolous lichen communities were sampled using a 10 x 10cm grid covering the lower 3m of each of 33 red oak (*Quercus rubra*) trunks in the vicinity of Douglas Lake, Northern Michigan. At each grid point the species of lichen present was recorded, in addition to it's nearest neighbour (the species of lichen nearest to and touching the sampled lichen with a 5cm radius), also the interaction between the two thalli (whether the thallus of one overtops the thallus of the other). As expected, the results show a non-random distribution of species on the tree trunk, both with respect to aspect and height, with the highest lichen biomass occurring on southerly aspects. Interspecific interactions are also non-random, with lichen species of high biomass/area ratio tending to overtop smaller species where they co-occur. This is extrapolated to reflect competitive abilities, based on the assumption that a thallus that overtops another is outcompeting it.

86

ECOLOGICAL AND PHYTOGEOGRAPHICAL DISTRIBUTIONS OF THE LOBATE SPECIES OF LECANORA LICHENS IN NORTH AMERICA. B. D. Ryan, Arizona State Univ., Tempe.

Lobate species of Lecanora lichens in western North America have several major ecological or phytogeographical distributions: 1) maritime areas in the Southwest (sect. Endochloris); 2) low elevation xeric woodlands of California (Lecanora mellea complex); 3) lowland deserts of the Southwest (L. bipruinosa and others); 4) upland deserts and xeric montane areas (many taxa); 5) montane to alpine areas (L. novomexicana and others). Some taxa found in both western and eastern North America (L. muralis, L. opiniconensis and L. valesiaca) occur at moderate elevations in inland areas (with the L. muralis complex also along the coasts), and others (e.g., L. straminea) occur only in maritime boreal-arctic areas. Sect. Dactylon occurs in the Arctic and in Mexico.

87

LICHENS OF GLACIER NATIONAL PARK, MONTANA. A.M. DeBolt, Oregon State Univ., Corvallis, OR.

Lichens were collected in Glacier National Park, Montana for a baseline species inventory. The park's designation as a UNESCO Biosphere Reserve and concerns of potential air quality degradation warranted a need for this information. Lichens were collected from as many different substrates, microhabitats, and elevations as possible. Ecological observations and relative abundance were recorded. To date, 326 taxa have been identified. Several species were found that are rare in the northern Rockies. Lobaria hallii, Collema curtisporum, and C. furfuraceum are apparently restricted to mature Populus trichocarpa trunks. The alpine species Alectoria nigricans, Umbilicaria havaasii, and Cornicularia normoerica are each known from only one site in the northern Rockies, all in Glacier National Park. Additional taxa will undoubtedly be located in the future.

88

THE RARE LICHENS PROJECT: DETERMINING A CONSERVATION STATUS. Sherry K. Pittam, Smithsonian Institution, Dept. of Botany, Washington D.C.

In June, 1989 a cooperative project between Dr. Mason E. Hale and Sherry K. Pittam of The Smithsonian Institution Department of Botany and The Nature Conservancy was begun to determine the conservation status of the approximately 3,400 species of lichens in North America. A report on the progress of The Rare Lichens Project is presented. Conservation status is largely determined by global range, overall abundance, threats to habitat or populations, and an estimate of the number of sites. This information is entered into a database. A combination of criteria, including limited or threatened habitat, small populations, narrow range, or a small number of known occurrences, is used to place species on the highest priority list. Examples include *Cladonia perforata, Gymnoderma lineare*, and *Phaeophyscia leana*. Due to incongruent criteria elements, status determination may be problematical. A Pacific Northwest forest endemic, *Lobaria oregana* is an example. It occurs in healthy, moderately abundant populations, but the habitat is both limited and threatened. Problems are also presented by the following: Taxa of disputed taxonomic rank or synonymy, chemical species, and newly described species. Problem resolution leads to a preliminary status determination, which can later be modified as more information is learned. A partial list of lichen species considered threatened or endangered is presented for comment.

89

THE PROCESS OF DUFF BURNOUT.
R.E. Martin and J. Scott, Univ. of Califor-nia, Berkeley.

Duff, the 02 and 03 layers of the forest floor, is generally considered to burn out from the top down. Obsevations over the years indicate duff to burn non-uniformly. Measurements indicate duff often burns horizontally from discrete ignition points where 1) irregularities such as holes, fissures, or rodent tunnels exist, or 2) ignition by surface fuels. Duff in a pine stand burned an average of 0.74 cm/hr with no wind and 2.68 cm/hr with winds at the surface of 6-9 km/hr. Duff depth consumption revealed a bimodal distribution, with the peaks being at about the 16 and about 60 percent of the original duff consumed. The process of duff consumption is understandable from a heat transfer standpoint, and may alter our thinking and models of the effects of fires on soils and flora.

90

Burning rate of smoldering peat.
W. H. Frandsen, Intermountain Fire Sciences Laboratory, Missoula, Montana

The rate of smoldering was examined using Canadian sphagnum peat moss as a representative fuel for forest duff. The time to burn a known amount of organic mass was monitored for different organic bulk densities, and moisture and inorganic contents. Organic bulk densities were comparable to the field and ranged from 90 to 180 kg m^{-3}. Moisture and inorganic contents, expressed as mass ratios relative to the organic mass, covered the range 0 to 0.8 for the moisture ratio, R_M, and from near zero (natural peat inorganic ratio) to 4.0 for the inorganic ratio, R_I. The burning rate, BR, is independent of the organic bulk density and can be expressed in the following manner:

$BR=7.58-2.72R_M-0.918(R_I-D)$ g h^{-1},

where $D=R_I$ if $R_I<1.0$ and

$D=1.0$ if $R_I \geq 1.0$.

91

FUEL CONSUMPTION AND FIRE BEHAVIOR ASSOCIATED WITH PRESCRIBED FIRES IN SAGEBRUSH ECOSYSTEMS.
D.B. SAPSIS and J.B. KAUFFMAN, Oregon State Univ., Corvallis.

There is little quantification of the dynamic relationships of fire and Artemisia tridentata-dominated ecosystems. Fuel loads, fuel moisture, climatic conditions, fire behavior and consumption were measured for experimental fires conducted during the spring and fall at the John Day Fossil Beds National Monument. Prior to fire, total aboveground biomass ranged from 6.2-10.6 mg ha^{-1}. Virtually all fuels were foliar, herbaceous or fine woody. (<7.6 cm diam.) materials. Given the fuel composition and vegetation structure of this ecosystem, fires can burn with great severity but this was found to vary depending on climatic and phenological conditions. In spring and fall burns, average flame lengths were 4.1 and 1.7 m and mean fireline intensity was 880 and 6400kW m^{-1} respectively. Mean biomass consumption in spring fires was 84% and in fall burns was 92%. Herbaceous moisture content was 143% and 9%, and sagebrush foliage moisture content was 186% and 97% at the time of the spring and fall prescribed burns, respectively. These differences in fire behavior and season of burn aid in the explanation of the often observed differences in ecosystem recovery following fire.

92

COMPARISON OF FUEL CONSUMPTION BETWEEN HIGH-INTENSITY FIRES AND MODERATE-INTENSITY FIRES IN LOGGING SLASH. J.N. Hall, USDA Forest Service, PNW Research Station, Seattle, WA 98105.

Slash burning is an integral tool of forest management in the Pacific Northwest. The purpose of this study was to determine if mass-ignited, high-intensity fires consume less fuel than moderate-intensity fires. The high-intensity burns used in the study consumed 23 percent less woody fuel, therefore diminishing one adverse effect of slash burning.

93

FIRE FREQUENCY EFFECTS ON NATURAL FOREST STRUCTURE IN THE SOUTHERN WASHINGTON CASCADES. A.N. Gray, Univ. of Washington, Seattle.

Multiple catastrophic fire events was investigated as a potential cause of wide age distributions in natural forests dominated by Douglas-fir (Pseudotsuga menziesii). Age and stand structure data were gathered in the Siouxon Ck. drainage, areas of which have burned at least twice since 1900. Fire boundaries and timing were inferred from historical records. Detail plots in multiple and single burn areas were paired by topography and plant association. Additional data were collected from reconnaissance plots and point samples. Fires appear to have been more frequent, and patchier in movement and intensity, at lower elevations. Several types of age distributions were found. Shrub and hardwood competition, wildlife foraging, and soil type had marked effects on stand structure. Fire frequency was an important factor, but had no consistent effect on age distributions.

94

FIRE HISTORY ON TWO SITES IN THE SISKIYOU MOUNTAINS, OREGON. J.K. Agee, University of Washington, Seattle.

Fire history was investigated on two sites in the Siskiyou Mountains: Kinney Creek in the Applegate River drainage, and Oregon Caves National Monument. The Kinney Creek area was photographed in 1917 and rephotographed in 1987. Fire frequency in this Douglas-fir type at about 1000 m elevation was about 15 years between 1760 and 1860 over about a 2 ha area, as measured by stump counts of fire scars. Photographs document other more recent fires that were not recorded on stumps. Oregon Caves, at elevations from 1300-1800 m, had conservative natural fire rotations from 60 years in the lower elevation Douglas-fir/oak community to 94 years in a higher elevation white fir/herb community, with substantial variation by century.

95

FIRE SEVERITY AND DAMAGE ON EXTENSIVELY - VERSUS INTENSIVELY-MANAGED LANDS WITHIN THE NORTH FORK FIRE, 1988. Philip N. Omi and Kostas Kalabokidis, Colorado State University, Fort Collins.

The Greater Yellowstone fires of 1988 provide an opportunity to study important distinctions between lands managed for preservation versus multiple uses. We surveyed fuel loadings, fire severity, and fire damage in extensively-managed, mature forests and in intensively-managed national forest plantations. Unburned, mature forests support higher fuel loadings in the duff and large fuel size classes. Fire damage was rated highest on 89% of the 55 mature forest plots, based primarily on crown scorch indicators. By contrast, highest fire damage ratings were associated with only 20% of the 45 plantation sites surveyed. Fire spread and damage were moderated in intensively-managed plantation areas. Intensively-managed forest areas improve fire management options in the Greater Yellowstone Area.

96

OVERCOMING THE PARADOX IN MANAGING WILDLAND FIRE. S.F. Arno and J.K. Brown, USDA Forest Service, Missoula, MT

Wildland fire management is a sound concept; but it is mired in a paradox: Protection of land and natural resources from fire over long periods has led to increased risk of severe fires and reduced resource values. The paradox is critically important in some ecosystems, but less important in others. We discuss this paradox by examining the basis for fire management and the barriers to its application in (1) "natural-process wildlands" such as Wilderness; (2) "resource-harvest wildlands," common in the national forests; and (3) "residential wildlands," an expanding zone near residences, resorts, and developments. Then we present possible approaches to restoring fire or substitutes for it and we argue that biologists and other natural scientists could play a pivotal role in achieving ecologically sound fire management. We focus on western North America, where federal wildlands are abundant and where fire is a prominent natural disturbance and initiator of successional change.

97

TAXONOMIC STRUCTURE OF PHYTOPLANKTON ASSEMBLAGES IN CRATER LAKE, OREGON.
C. D. McIntire and M. Debacon,
Oregon State Univ., Corvallis.

A taxonomic analysis of 171 phytoplankton samples obtained from Crater Lake, Oregon, between 1985 and 1987 revealed 132 taxa in the upper 250 m of the water column. Phytoplankton cell biovolume in the upper 20 m of the water column was relatively high during the summer months, a time period when Nitzschia gracilis was dominant in the epilimnion. Cluster analysis identified a sparse, temporally ubiquitous flora which was modified to various degrees when environmental conditions became favorable for the growth of a few dominant taxa. These surges of dominance by individual taxa accounted for 2 to 5-fold increases in cell biovolume and generated a pronounced taxonomic discontinuity between the floras in the epilimnion and hypolimnion.

AUTHOR INDEX TO ABSTRACTS

Numbers identify abstract by their unique number, not by page numbers.

Agee, J.K. 94
Alaback, P.B. 16
Anderson, N.H. 59
Antieau, C. 70
Arno, S.F. 96
Arthurs, J. 28
Askham, L.R. 47

Bahls, P.F. 62
Bedunah, D.J. 12
Benson, G.L. 24
Boyle, J.R. 54
Brown, J.K. 96
Bush, J.L. 45

Cai, Y.C. 30
Caicco, S.L. 71
Camm, E.L. 33
Campbell, D.L. 43
Chambers, C. 44
Chanway, C.P. 34
Charleson, L. 36, 37, 38, 39, 40
Chen, J. 17
Clark, D.L. 64
Clatterbaugh, K.C. 20
Cole, E.C. 1
Concannon, J.A. 16, 20
Crampton, D. 31
Crawford, D.L. 56
Cromack, K., Jr. 56
Crooks, F.B. 53
Cummings, S.A. 41

Dambacher, J.M. 60
Davis, J.R. 83
Debacon, M. 97
DeBolt, A.M. 87
Denison, W.C. 81
Dieterich, M. 59
Donnelly, P.K. 56

Eddleman, L.E. 9, 10
Edmonds, R.L. 11
Emmingham, W. 6
Enns, K.A. 80
Entry, J. 6, 56

Fangen, W.V. 2
Farley, J.P. 43
Frandsen, W.H. 90
Franklin, J.F. 16, 17

Gaines, W.L. 45
Garcia, E.R. 45
Gibbons, S. 58
Gillies, S.L. 32
Gilliland, L.L. 12
Giordano, P. 4
Gray, A.N. 93
Griffith, J.A. 52
Guy, R.D. 13, 74

Hall, J.N. 92
Hallett, J.G. 41, 42
Hanley, D.P. 5
Hann, D.W. 3
Harper, G. 33
Harrington, T.B. 8
Harrison, R. 57
Hawkins, C. 58
Henry, C.L. 57
Hibbs, D.E. 3, 4
Hinckley, T.M. 15
Holowachuk, D. 13
Hospodarsky, D.C. 49
Hubbard, C.J. 72
Huff, M.H. 26
Hughes, T.F. 8
Hurley, M.D. 63
Husted, L.D. 35

Ingersoll, C.A. 65
Isik, K. 29

Jackson, P.L. 52
John, E.A. 85

Kalabokidis, K. 95
Kauffman, J.B. 91
Kaya, Z. 29
Kaye, T.N. 66
Kiemnec, G. 67
Kramer, S. 9, 10
Kwiatkowski, S. 73

Larson, D.W. 61
Larson, G.L. 58
Larson, L.L. 67, 68
Lavender, D.P. 31, 36, 37, 38, 39, 40
Leavell, D.M. 72
Liss, W.J. 63
Liu, X. 30
Lomnicky, G.A. 63
Long, W.A. 50
Lowe, J.S. 19

Martin, R.E. 89
McComb, W. 44
McCune, B. 78, 79
McInnis, M.L. 68
McIntire, C.D. 97
McIver, J.D. 46
McShane, C. 70
Miller, P.M. 10
Miller, R.F. 7, 68, 98
Minore, D. 21
Moldenke, A. 46, 54
Murray, M.D. 25

Newton, M. 1, 44, 51

O'Connell, M.A. 42
Omi, P.N. 95

Parsons, G.L. 46
Phillips, E.C. 48
Pittam, S.K. 88
Puettman, K.J. 3

Radwan, M.A. 2
Riegel, G.M. 7
Rust, S.K. 23
Ryan, B.D. 86

Samora, B. 58
Sapsis, D.B. 91
Scott, J. 89
Segura, G. 15
Sharrow, S. 6
Shaw, C.H. 54
Shaw, D.C. 28
Sherwood-Pike, M. 84
Silim, S.N. 36, 37, 38, 39
Sillett, S.C. 81, 82
Southworth, D. 73
Spies, T. 17
Sprague, A. 45
Stone, D.F. 78

Tappeiner, J.C., II 8
Thomas, T.B. 11
Thompson, R.L. 69
Tung, C.H. 29
Turpin, D.H. 74

Van Pelt, R. 18, 27
Vance, N.C. 75
Vidaver, W.E. 32

Wagner, O.E. 55,77
Wagner, R.H. 76
Wang, Z.Q. 30, 51
Webb, W.L. 14
Weger, H.G. 74
Wilson, M.V. 64, 65
Wright, G. 15

Xue, D. 57

Zaerr, J.B. 30
Zasada, J. 22

KEYWORD INDEX TO ABSTRACTS

Numbers identify abstracts by their unique numbers, not by page numbers

Abies amabilis 15
Acidic deposition 12
Acidic fog 12
Allocation 9, 10
Alluvial 18
Alpine 65, 66

Bacillus 34
Brachypodium sylvaticum 72
Bedrock 51
Biomass 9
Botany 87
Branching 78

Calochortus nitidus 71
Canopy 81
Cardaria draba 68
Cedar 39
Chemistry 11
Christmas trees 5
Clearcutting 46
CO_2 enrichment 13
Cold hardiness 36, 38
Cold storage 37
Communities 63
Competition 4, 7, 8
Computer taxonomy 54
Conifer utilization 25
Conservation 70, 88

Data loggers 47
Decline 15
Decomposition 56
Deposition 11
Desert shrubs 30
Distributions 86
DNA fingerprinting 41
DNA probe 41
Dormancy induction 32
Douglas-fir 43, 80, 93, 94
Dryden rhythmites 50
Duff burnout 89

Ecological value 26
Ecosystem analysis 19
Edges 16, 17
Environmental sensitivity 29
Environmental stress 23
Epiphytes 84
Evernia 78, 79

Fertilization 5
Fire 89, 90, 91, 93, 95, 96, 98
Fire history 94
Forest 17
Forest fragmentation 16
Forest Service 20
Frost hardiness 39
Fuel consumption 92
Fungi 84

Germination 22, 67
Gravity 55
Green algae 74
Growth model 8

Habitat 60

Illinois 53
Inoculation 34
Insect life histories 59
Inventory 45

Lake 63, 97
Land use planning 52
Lead accumulation 79
Lichens 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88
Light intensity 31
Lignin 56
Limnology 61

Management 96
Meadowfoam 73
Microtine rodent 42
Mitochondria 74
Mixed stands 3
Modeling 14, 49
Mortality 27
Mountain lake 62
Mycorrhizae 35
Myrtle Island 69

Nutrient 76

Off-road vehicles 48
Old-growth 26, 27, 82
Osmotic 67

Pacific yew 25
Philosophy 20
Photoperiod 36, 37
Photosynthesis 14, 76
Phytoplankton 61, 97
Picea engelmannii 13
Pinus brutia 29
Plant community 23, 24
Planting patterns 6
Planting stock 2
Population model 42
Prescribed fire 92
Presettlement forest 53
Proteins 75

Quercus garryana 83
Quercus rubra 85

Rare plant 70
Recreation 48, 49
Red alder 1, 2, 4, 44
Repellent 43
Riparian 21
Root growth 33
Root:shoot 10

Sagebrush 91
Sap flow 77
Seed dormancy 66
Seed weight 22
Seedbank 64, 65
Seedling growth 40
Self-thinning 3
Sewage sludge 57
Site preparation 40
Smolder 90
Soil fauna 54
Soil moisture potential 31
Spotted owl 45
Spruce 33, 35
Stand dynamics 19
Steelhead 60
Stream 58
Succession 18, 46, 64

Temporary streams 59
Tissue culture 73
Transpiration 51
Tree growth 6
Trout 62

Understory 7

Vegetation 21, 24, 69
Vertebrate abundance 44

W-waves 55, 77
Water deficit 75
Water quality 58
Water stress 30
Weed control 68
Western hemlock 1, 28
Western juniper 98
Wetlands 52
Wetwood 28
White spruce 32, 38

Yellowstone 95

ACKNOWLEDGEMENTS

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1990

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May 1990 Volume 64, Number 3

WINNERS OF RESEARCH GRANTS

NORTHWEST SCIENCE

CONTENTS

Announcements

121 Mass Balance of the Taku Glacier, Alaska from 1946 to 1986—**M. S. Pelto and M. M. Miller**

131 Recovery of Douglas-fir Seedlings from Logging Damage in Southwestern Oregon: Preliminary Evidence—**Steven D. Tesch and John W. Mann**

140 Frost Distribution and Occurrence on a Rangeland Watershed in Southwest Idaho—**Dennis Burton, Clayton L. Hanson, and Myron Molnau**

150 Recharge Estimates for the Hanford Site 200 Areas Plateau—**R. C. Routson and V. G. Johnson**

159 Avalanche-Generated Debris Flow of 9 May 1986, at Mount St. Helens, Washington—**Kenneth A. Cameron and Patrick T. Pringle**

165 Lithofacies and Sedimentology of the Miocene-Pliocene Ringold Formation, Hanford Site, South-Central Washington—**Kevin A. Lindsey and David R. Gaylord**

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May 1990 Volume 64, Number 3

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CONTENTS

Announcements

121 Mass Balance of the Taku Glacier, Alaska from 1946 to 1986—**M. S. Pelto and M. M. Miller**

131 Recovery of Douglas-fir Seedlings from Logging Damage in Southwestern Oregon: Preliminary Evidence—**Steven D. Tesch and John W. Mann**

140 Frost Distribution and Occurrence on a Rangeland Watershed in Southwest Idaho—**Dennis Burton, Clayton L. Hanson, and Myron Molnau**

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Announcements

The 63rd Meeting of the Northwest Scientific Association

The annual meeting of the Northwest Scientific Association was held in March at Oregon State University. Among other activities, the symposium entitled "Natural Disasters: The Nature of Recovery" was a large success. Speakers covered a variety of topics and seemed to draw much interest from the audience. The symposium received both radio and television coverage. Contributed papers included a diversity of topics from lichen ecology to solar energy. The field trips were fully subscribed.

The Association presented its outstanding Scientist Award to Dr. Richard Waring, of Oregon State University. The research interests of Dr. Waring have centered upon examining the functioning of ecosystems with special emphasis on indexing moisture and heat stress. In recent years he has employed remote sensing of plant communities in the classification of wildlife and forest resources.

Five research awards to students were awarded to the following:

- *Vincent A. Cobb.* Daily and Seasonal Variation in the Activity Patterns of Great Basin Rattlesnakes. Dept. of Biological Sciences, Idaho State University, Pocatello, ID 83209. Major Professor: Dr. Charles R. Peterson.

- *Richy J. Harrod.* The Pollination Ecology of *Certaurea diffusa* Lam. (Compositeae). Biology Department, Western Washington University, Bellingham, WA 98225. Major Professor: Dr. Ronald J. Taylor.

- *Jay Goodwin.* The Ecological Role of *Vesicular arbuscular* mycorrhizae in the Restoration of Degraded rangelands. Department of Rangeland Resources, Oregon State University Corvallis, OR 97331. Major Professors: Dr. Paul Doescher and Dr. Lee Eddleman.

- *Lauri E. Mackelburg.* The Effects of Habitat Patchiness on the Spatial Distribution and Social Organization of Microtine Rodents. Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410. Major Professor: Dr. James G. Hallett.

- *Leslie Richman.* The Role of Learning: Diet Training as a Means Toward Manipulation of Habitat Through Livestock Management. Department of Rangeland Resources, Oregon State University, Corvallis, OR 97331. Major Professor: Dr. Douglas E. Johnson.

M. S. Pelto, Nichols College, Department of Environmental Science, Dudley, Massachusetts 01570

and

M. M. Miller, Foundation for Glacier and Environmental Research, Moscow, Idaho 83843

Mass Balance of the Taku Glacier, Alaska from 1946 to 1986

Abstract

The Taku Glacier is a temperate, maritime glacier of the Juneau Icefield, southeast Alaska. This glacier is the largest of the icefield, and has advanced 6.8 km since 1890, 1.6 km since 1948. The mass balance record of the Taku Glacier (1946-1986) indicates that the glacier's continued advance has been due to positive mass balance. The mean annual balance during the 1946-1986 period was $+0.37 \pm 0.06$ meters/year (m/a) of water equivalent. Due to the large surplus balance of the previous 40 years the Taku Glacier will continue to advance for the remainder of this century.

Introduction

Since 1946 the Juneau Icefield has been the site of extensive annual field measurements conducted by the Juneau Icefield Research Program (JIRP). In 1949 JIRP came under the aegis of the American Geographic Society with support from the Office for Naval Research (ONR). After completion of the ONR contract in 1957, support was received from the Foundation for Glacier and Environmental Research. Since then JIRP has been under the direction of Maynard Miller. Annual field measurements include determination of the equilibrium line altitude (ELA), balance gradient, glacier surface velocity, glacier surface level, heat balance, surface meteorology and terminus fluctuations. The main emphasis has been on the Taku Glacier (Figure 1 and 2), the icefield's largest glacier (671 km^2).

Taku Glacier is divided into three zones: the ablation zone (113 km^2) below the equilibrium line altitude (ELA), the lower neve region (178 km^2) extending for 400 m in elevation above the ELA, and the upper neve region (380 km^2) occurring more than 400 m above the ELA. These are climatic zones. The ablation zone is primarily sensitive to ablation season temperature, the upper neve zone is primarily sensitive to accumulation season precipitation, and the lower neve zone is sensitive to both accumulation season precipitation and ablation season temperature. Taku Glacier has eight primary tributaries and two terminus tongues; the main glacier terminus and the Hole-in-the-Wall terminus. The Hole-in-the-Wall Glacier branches off of the main Taku Glacier, five kilometers from the main terminus. In this study the Hole-in-the-Wall Glacier is not referred to separately since in a mass balance assessment it is part of the Taku Glacier.

Mass Balance Measurement Methods

The mass balance measured on the Taku Glacier is a surface balance. The techniques used are the standard stratigraphic methods described in detail by (LaChapelle 1954, Miller 1956, Nielsen 1957, Hubley 1957, Heusser and Marcus 1964), and described briefly below. The measurements are carried out from late June through mid-September, thus actual winter (October-April) and summer (May-September) balance are not determined, only annual balance is determined. The annual balance of the Taku Glacier is largely based on measurements at 19 fixed sites conducted at the same time each year, using the same methods.

In the accumulation zone snowpits and crevasse stratigraphy are used to determine snow depth. Water equivalent is measured in a continuous vertical profile through the annual snow layer. Probing is not an accurate technique due to the presence of ice lenses. In the ablation zone, ablation stakes are drilled into the firn or ice and the surface ablation measured. The product of surface density and surface level change yields ablation. It must be emphasized that ablation records seldom span the entire ablation season.

A number of additional techniques have been used in recent years to reduce and better understand the sources of errors in employing the above methods of annual balance measurement. Ablation triangles are used to determine annual ablation instead of individual ablation stakes. Each ablation triangle consists of three stakes

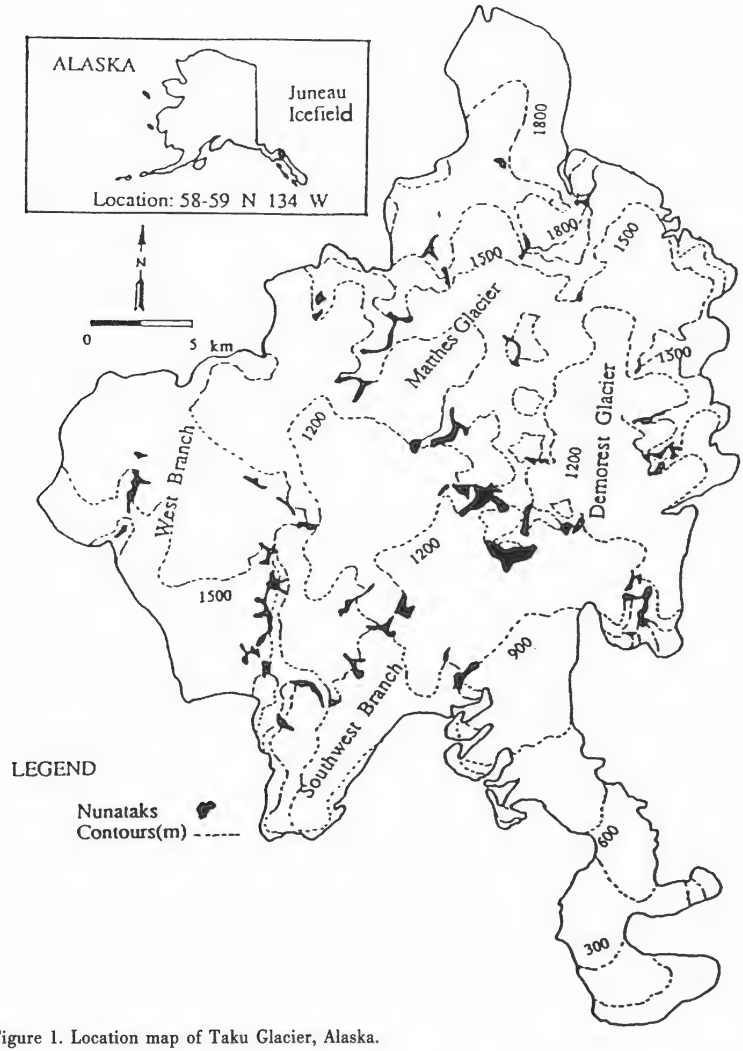


Figure 1. Location map of Taku Glacier, Alaska.

driven or drilled into the glacier 3 m apart, forming an equilateral triangle. Hubley (1957) pointed out the major sources of error associated with using ablation stakes: failure to measure density, failure to monitor the water content of the entire accumulation layer, and the use of data from only one point on a variable glacier surface. To reduce such errors, daily measurements of surface ablation are made at nine locations on the triangle perimeter. The mean surface ablation value is multiplied by the measured surface density to obtain ablation. This method indicates an increased variance of 0.01 m/day in ablation determination using a single point versus using multiple points. This error compounded daily would result in significant cumulative error for the entire ablation season.

The major error in the ablation studies arises from inability to conduct studies at the beginning and conclusion of the ablation season on an annual basis. Extrapolations are used based on data from multi-year ablation studies and

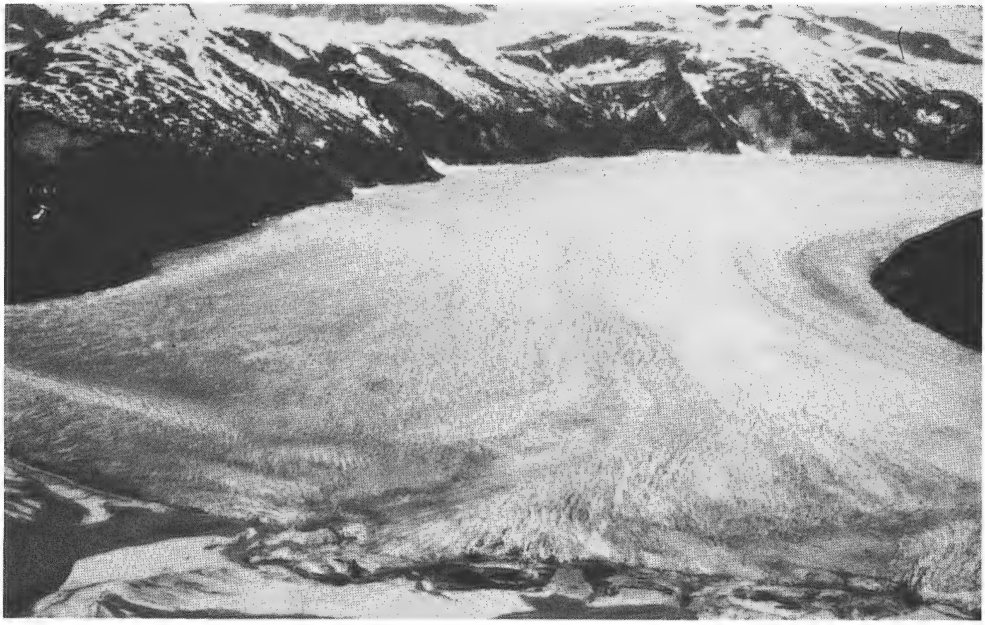


Figure 2. Terminus of the Taku Glacier in 1981.

ablation studies that have continued into the accumulation season in 1950, 1951, 1952, 1964, 1961, 1965, 1973, 1974, and 1982 (Miller 1956, Miller 1963). The second major error is the sparseness of ablation measurements.

Errors in mass balance calculation due to not considering internal accumulation on Alaskan glacier are significant (Mayo and Trabant 1984). Internal accumulation is the refreezing of meltwater within the snow and firn pack. Only meltwater that escapes the glacier is ablation. Internal accumulation is estimated based on bulk density measurements of the upper four accumulation layers. Correlation of stratigraphic layers on a yearly basis indicates that in the first three years after burial the accumulation layer will receive from downward percolation approximately the amount of meltwater that the layer lost while at the surface. Due to densification and diagenetic structures impeding flow, there is negligible percolation through more than the first four annual layers. This attribute has been noted on temperate glaciers in the Caucasus Mountains as well (Bahzev 1986). On the Taku Glacier above 1600 m ablation is limited as most meltwater is retained in the snow and firn pack as internal accumulation. Internal accumulation increases with elevation, comprising 10 percent of the annual accumulation at 1000 m, 10-14 percent at 1200 m and 15-21 percent between 1400 m and 2100 m (Leighton 1952, Miller 1963). Below 1400 m much of the meltwater escapes the glacier system quickly and is ablation.

Errors can arise in accumulation measurements due to small scale variations of firn-snowpack depth and density. To determine this error the snowpack depth and density was checked at 40 locations in a 1000 m^2 area at different elevations and in different years (Pelto 1984). The standard deviation was only ± 0.07 m of water equivalent in a 1 to 2 m snowpack. As noted by (LaChapelle 1954, Hubley 1954, Miller 1956), the density of the summer snowpack on the Taku Glacier is a remarkably uniform 0.54-0.62 kg/m during the latter portion of the ablation period, from the surface to the base of the annual accumulation layer.

Spot measurements of mass balance can be extrapolated on Taku Glacier because of the consistency of accumulation and ablation over

sizable areas. In the accumulation zone this is largely due to the fact that wind drifting and avalanching are not important sources of accumulation. The comparatively smooth surface of the Taku Glacier results in even deposition, erosion and melting of the snowpack. During the majority of the ablation season, low complete cloud cover persists. The result is a uniform heat budget, and consequently uniform ablation at the surface of the glacier over regions at the same elevation. These factors allow a lower sampling density in mass balance determination on the Taku Glacier than is typical.

Annual Balance Calculation

The methods described above have not always been strictly followed by the several hundred researchers who have gathered mass balance data on the Taku Glacier. The methods do allow use of less comprehensive data as 40 years of study has yielded an excellent understanding of the mass balance variation on the Taku Glacier and problems in measuring it. Although no mass balance results have been previously published for the Taku Glacier, now after 40 consecutive years of extensive measurements sufficient mass balance data exists to accurately reconstruct the annual balance history of the Taku Glacier for the 1946 to 1986 period.

The Taku Glacier mass balance record is the longest in North America. However, the record must be treated with care as there are limitations to the accuracy of the record. Despite the inaccuracies this record is a valuable climatic record for the Coast Range of Alaska.

Limitations to the mass balance record are: (1) The density of measurements averages 1 per 13 km^2, and are particularly sparse in the ablation zone. (2) Measurements are usually concluded by early September. At this time the accumulation season has begun in the accumulation zone, but not in the ablation zone. (3) Data acquisition in the ablation zone does not usually extend over the entire ablation season and is often not undertaken on the lower 12 km of the Taku Glacier. (4) Measurements have been carried out by several hundred different researchers.

However, mitigating these limitations are: (1) Since 1946 measurements have been completed annually at 18 specific locations on the Taku Glacier (Figure 3). Measurements at these 18 sites

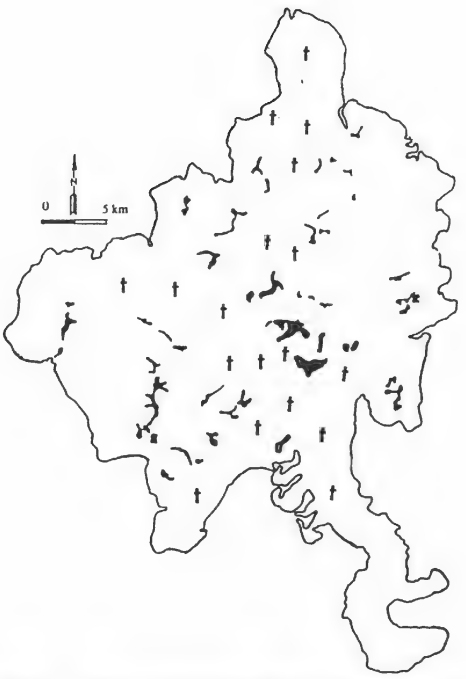


Figure 3. Location of the 18 sites where annual mass balance measurements have been completed since 1946.

are completed each year using the same methods at the same time of the year. Each year these measurements are supplemented by other measurements, but the balance gradient used in reconstructing annual balance is largely based on these 18 measurement sites. The mass balance calculations are then consistent and precise. Climatic interpretations are not limited by the aforementioned systematic errors. (2) Measurements carried out throughout the ablation season in nine different years are used to extrapolate ablation data to the end of the ablation period. (3) The balance gradient of the Taku Glacier in the ablation zone has a constant shape that is known, but does shift with respect to altitude (Mayo 1984, Pelto 1987). The balance gradient shape is fixed with respect to elevation annually using the ELA. Thus, the ablation rate at any elevation can be determined. (4) Errors due to the number of researchers is limited by the fact that all are trained to use the same methods, and that at least one experienced researcher supervises each measurement.

All available mass balance measurement data are used to construct a mean mass balance gradient and mass balance map for the entire glacier (Figures 4 and 5). Mass balance data for each individual year was compiled and contoured. In areas where data gaps exist mass balance contours are extrapolated, based on the mean mass balance contour pattern, with the magnitude of each mass balance contour adjusted to fit the existing data from that year (Figure 5). A mean mass balance map for the entire glacier is completed and the mass balance for the glacier is calculated by integration.

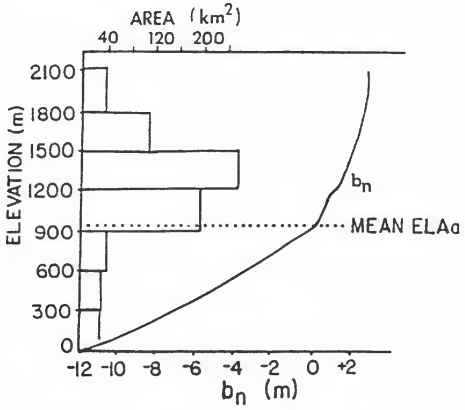


Figure 4. Balance gradient and area elevation curve for Taku Glacier.

The annual balance (bn), the sum of the products of the mean annual balance (bz) and the glacier surface area (Az) within each 160 m elevation zone of the Taku Glacier (Figures 4 and 5). Equation 1 is used to calculate annual balance.

$$bn = Az\ bz/At \quad (1)$$

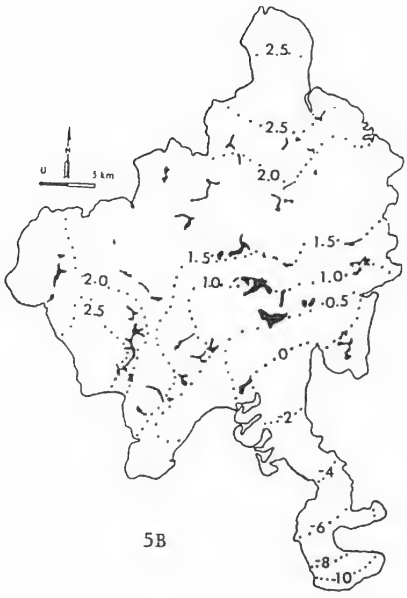
In equation 1, At is the total glacier area. Standard errors reported are for one standard deviation of the observed fluctuation in direct mass balance measurements. Below the ELA on the Taku Glacier mass balance calculations rely solely on ablation studies, with an estimated average annual balance error of ± 0.20 m. The lack of measurements in the ablation zone cause a high but systematic error. The error is again limited by the uniformity of ablation which can be accurately estimated from the observed balance gradient. In the lower neve zone the average error is ± 0.15 m, due primarily to the failure in conducting measurements to the absolute conclusion of the ablation season. The upper neve zone has an error of ± 0.10 m resulting from a lower than ideal sampling density. All of the latter errors are random. The error in annual balance measurements for the entire Taku Glacier is ± 0.14 m, dropping to ± 0.08 m for any given ten-year period. The annual balance record for the Taku Glacier during the 1946-1985 period is shown in Table 1.

Mass Balance and Climatic Trends

The mass balance record of the Taku Glacier from 1946-1986 can be divided into six segments (Figure 6). (1) 1946-1949 was a period of positive annual balance, resulting from high winter cyclonic activity. (2) From 1950 to 1957 a period of negative annual balance due to below normal accumulation temperatures was associated with decreased cyclonic activity. (3) The 1958-1962 period had increasing annual balances as winter temperature and precipitation increased. (4) During the 1964-1975 period, cool ablation season temperatures and above average winter precipitation caused large surplus annual balances. The low winter temperatures of this period were noted throughout the northern hemisphere, in an analysis of 191 weather stations, and did not reflect decreased cyclonic activity (Kelly *et al.* 1982). (5) From 1976 to 1983 temperatures rose rapidly during both accumulation and ablation seasons. The increased ablation offset increased accumulation, and low surplus annual balances resulted. (6) 1984 through 1988 was a period of extreme positive mass balance, caused by record winter warmth and high accumulation season cyclonic activity. The prevailing wind direction shifted for the first time since 1946 from southeast to east-southeast. The true nature and cause of this last climatic fluctuation are not yet clear.

Each of the six periods mentioned above indicates a change in local weather noted in Juneau and a change in mass balance on the Taku Glacier. This analysis demonstrates that Juneau weather records can be useful in predicting glacier regimen for Taku Glacier if fluctuations in weather caused by local, regional or global scale variation of atmospheric circulation are distinguished.

5A



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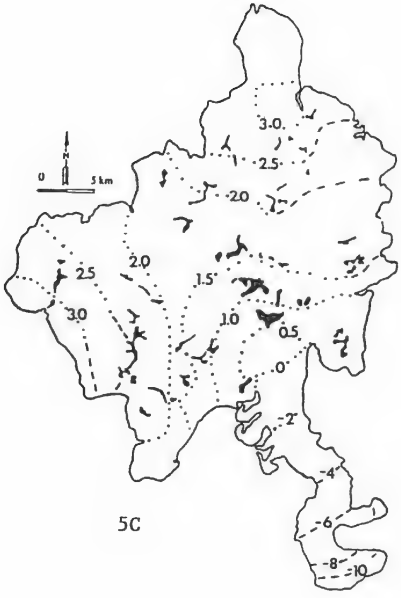

5C

Figure 5a. 1962 mass balance map of the Taku Glacier, in meters of water equivalent. Measurement sites indicated by t.
5b. Mean mass balance map of Taku Glacier (1946-1986).
5c. 1962 mass balance map of the Taku Glacier used to calculate annual balance. This is a composite of 5a and 5b. The contour pattern in 5b is used to fill in data gaps in 5a. The magnitude for these contours are assigned based on data from neighboring points.

TABLE 1. The annual equilibrium line altitude (ELA), annual net balance (b_n) in millimeters of water equivalent and number of measurement sites for the Taku Glacier, Alaska from 1946 to 1986.

Year	ELA	b_n	Data points
1946	980 m	— 40 mm	38
1947	900	360	40
1948	870	510	43
1949	800	930	71
1950	1010	—180	74
1951	1160	—340	79
1952	950	160	93
1953	1010	—150	82
1954	980	— 70	57
1955	780	970	34
1956	1000	—130	37
1957	1010	— 40	35
1958	930	210	63
1959	915	350	59
1960	950	160	51
1961	885	480	47
1962	900	390	71
1963	875	570	41
1964	750	1130	62
1965	810	790	57
1966	965	80	48
1967	930	250	53
1968	885	460	46
1969	730	1170	44
1970	825	760	37
1971	850	630	56
1972	880	420	35
1973	870	520	39
1974	850	580	44
1975	800	850	52
1976	850	660	38
1977	885	470	49
1978	915	310	47
1979	950	140	34
1980	870	540	38
1981	980	120	43
1982	950	150	91
1983	1085	—420	86
1984	875	640	178
1985	600	1400	39
1986	720	1200	43
Mean	910	370	55

Recent Glacier History

The mass balance of southeast Alaskan glaciers is dictated by (1) the calving flux, (2) the percentage of a glacier's total area within the maximum accumulation area (MAA) and, (3) most importantly, the accumulation area ratio (AAR). AAR is the percentage of a glacier's total area above the ELA (Meier and Post 1962). AAR is reported as a percentage. In southeast Alaska the maximum accumulation zone is the region where mean accumulation season temperatures are —5 to —11°C (Pelto 1987). Changes in the regimen of glaciers that are not surging occur only when AAR and MAA cross threshold values necessary to maintain equilibrium (Mercer 1961). Below the threshold values negative mass balances cause glacier retreat. Above the threshold values positive mass balances lead to glacier advance. The Taku Glacier is not a surging glacier and has had a negligible calving rate since 1946. Thus, only AAR and MAA determine its present behavior. The threshold value for AAR and MAA are 67 and 50 for a low calving rate or non-calving glacier (Pelto 1987).

The Taku Glacier and its distributary tongue the Hole-in-the-Wall Glacier began advancing in the 1890s from a retracted position. At this time the glacier had an AAR of 88 and a MAA of 64, more than sufficient to maintain a strong advance behind the protective terminus shoal built by the glacier (Field 1952). The advance continued behind the progressing terminus shoal, which was effectively a push moraine (Miller 1963). By 1948 the main terminus had advanced 5.3 km from its retracted position, a rate of 88 m/year, and was no longer calving. The AAR was 86 and the MAA was 63 providing a strong positive mass balance that has driven an additional 1.5 km advance of the main terminus since 1948, a rate of 37 m/year. Today the Taku Glacier does not calve and with an AAR of 82 and a MAA of 62 still has a strong positive mass balance, which will enable the glacier to advance for the remainder of this century. The Taku Glacier is in the advance stage of the Alaskan tidewater glacier advance-retreat cycle, and is comparatively insensitive to climate at present. Figure 7 shows the terminus behavior of the Taku Glacier, Hole-in-the-Wall Glacier, and Norris Glacier since 1890. The Hole-in-the-Wall terminus has advanced 3.2 km since 1890, at a rate of 33 m/year. The Hole-in-the-Wall Glacier is a spillover tongue of the Taku Glacier and has a parallel history. The Norris Glacier has an AAR of 61 and a MAA of 38, values that are well below equilibrium threshold values, resulting in 1.8 km retreat since 1890.

The reduced advance rate of recent decades is caused by the expanding terminal front (Field 1952, Miller 1963), not declining mass balance. Heusser (1952) attributed the Taku Glacier's advance to a series of ice waves and not to positive

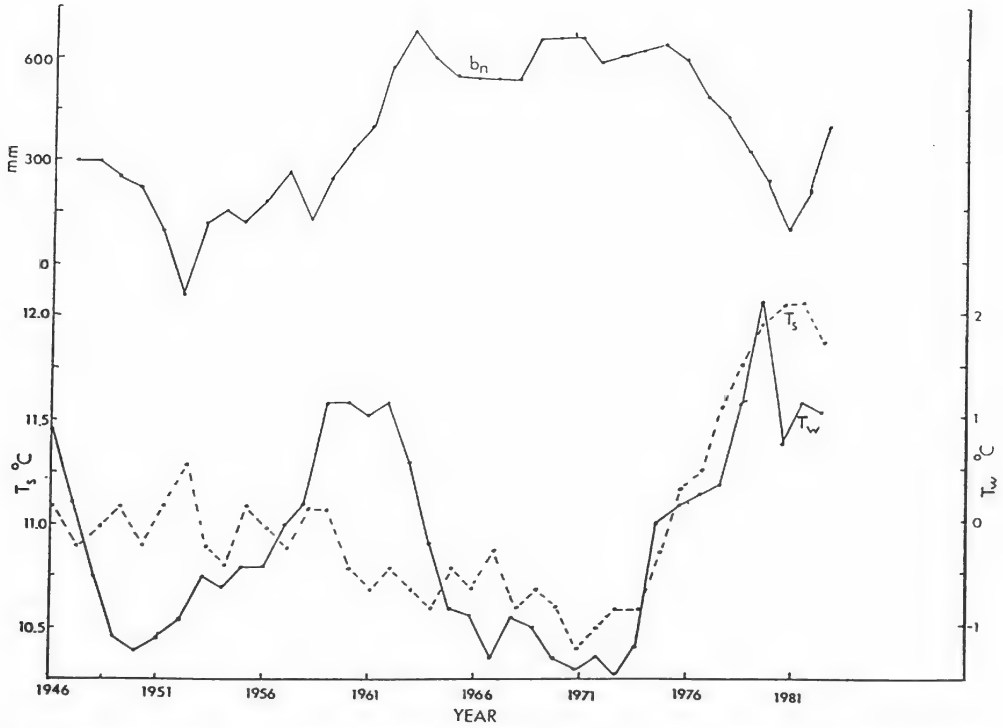

Figure 6. Five year running mean of accumulation season temperature (Tw), ablation season temperature (Ts) and mass balance (bn) of Taku Glacier.

mass balance. Small ice waves are present 10 to 20 km above the terminus, but they are infrequent and not of a scale that could cause a continuous advance over a period of thirty years. It is evident that the advance of the Taku Glacier is due to a positive mass balance.

Summary

The annual balance record for the Taku Glacier assembled from existing JIRP data provides the longest continuous record in North America. The Taku Glacier has had a positive balance for almost the entire period (Figure 6). The mean annual balance during the 1946-1986 period on Taku Glacier has been +0.37 m/year ± 0.06 m/year. The positive mass balance of the past forty years will allow the glacier to continue to advance for the remainder of this century regardless of climatic variations.

The annual balance record for the Taku Glacier and Juneau weather records indicate a significant climatic fluctuation beginning in 1976. Temperatures increased sharply for each season of the year in the Arctic Basin during this period (Kelly *et al.* 1983). The true nature of the climatic trend is not clear. What is clear are the unparalleled extremes of climate in southeast Alaska during the last decade.

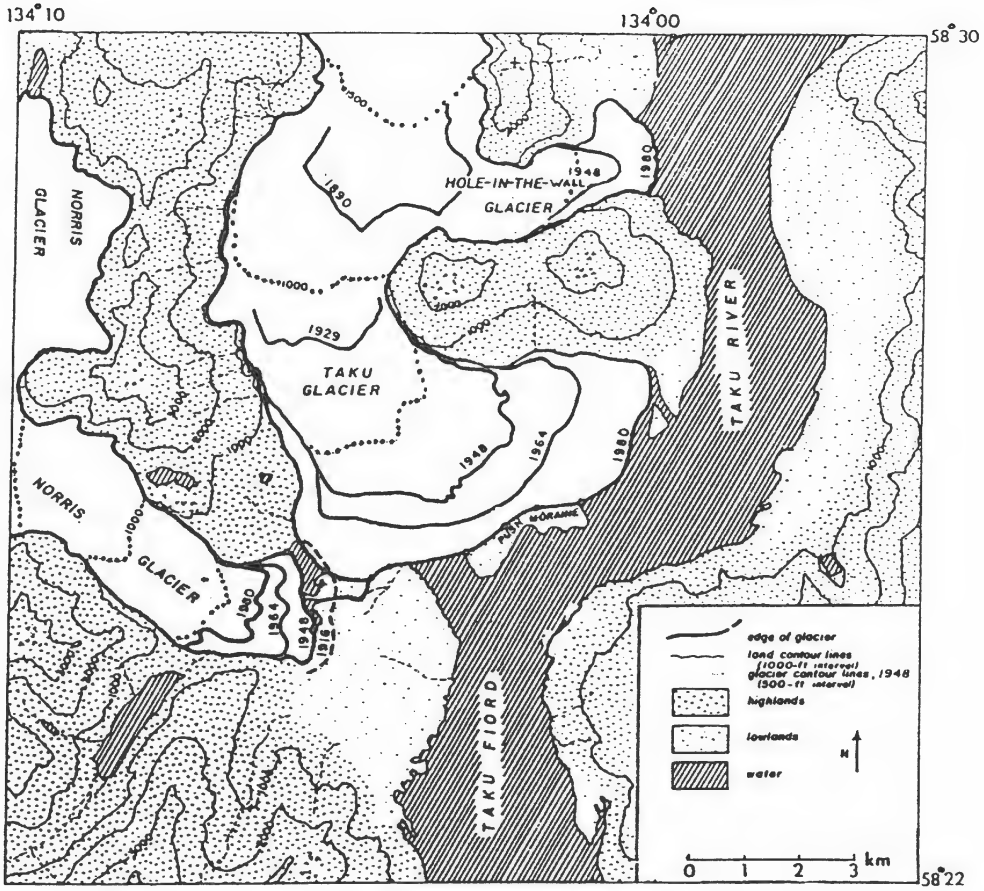

Figure 7. Terminus behavior of Taku Glacier, Norris Glacier and Hole-in-the-Wall Glacier.

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Received 19 January 1989
Accepted for publication 6 December 1989

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Recovery of Douglas-fir Seedlings from Logging Damage in Southwestern Oregon: Preliminary Evidence

Abstract

Two studies involving overstory removal in shelterwood stands of southwest Oregon indicate that Douglas-fir understory reproduction up to 4.5 m tall can recover from substantial logging-related injuries. In these studies, such injuries included breakage of stems or terminal leaders, as well as wounds covering up to half the stem circumference. In one study, remeasurement 3 growing seasons after overstory removal indicated that at least 75 percent of the damaged seedlings that were initially 60 cm tall or taller could be classified as crop trees. At that time, annual height growth did not differ significantly between undamaged trees and those with small stem wounds or stem breakage near the top of the tree. Only when logging damage had been severe, with seedlings pushed over and sometimes still pinned to the ground, was height growth significantly less. In a second study, seedlings less than 30 cm tall recovered poorly from logging injuries and died more often than larger seedlings.

The present database is limited and caution should be exercised in using it to predict seedling recovery after other harvesting operations; however, it appears that a classification system based on seedling damage sustained during logging can be useful in predicting subsequent recovery.

Introduction

In the western United States, forest stands are often regenerated by the shelterwood system, which involves removal of mature timber in a series of cuttings so that seedlings can become established under the partial shelter of overstory trees. Today, shelterwood stands in this region cover hundreds of thousands of hectares, and many are ready for overstory removal (U.S. Department of Agriculture 1979, Lysne *et al.* 1982). The challenge in harvesting these stands varies greatly, depending on terrain, management history, number of overstory trees to be removed, and number of seedlings established in the understory (Mann and Tesch 1985). Furthermore, overstory removal in shelterwood stands always causes some damage and mortality to seedlings. If a site is excessively stocked, seedling mortality caused by logging can result in beneficial thinning (Barrett *et al.* 1976). However, if stocking is barely adequate before overstory removal, maintaining an adequate number and distribution of seedlings can be critical. Unfortunately, little information is available to help forest managers predict recovery potential of conifer seedlings damaged during overstory removal.

When stocking is marginal after logging, foresters could make better decisions if they knew the number of damaged seedlings that will recover to crop tree status, length of the recovery period, and growth rate of damaged seedlings in comparison with that of undamaged ones. Reliable prediction of seedling recovery could assure managers that stands meet minimum targets for stocking and that replanting is unnecessary.

This paper reports on two studies dealing with survival and recovery of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) seedlings after overstory removal in shelterwood stands of southwest Oregon, focusing specifically on the fate of regeneration beyond direct harvesting-related mortality. The Grub Gulch (GG) case study was begun in 1980 to identify seedlings characteristics and logging factors that influence seedling survival during overstory removal (Tesch *et al.* 1986a). While the original study was not designed to measure recovery, understory seedlings were permanently marked prior to overstory removal, allowing remeasurement of the survivors in 1984. These remeasurements enabled us to relate seedling recovery (crop tree status and growth rate) to severity of logging injury and seedling size before logging. A longer-term study on Douglas-fir seedling recovery (DFSR) was subsequently started in 1984 across a broader range of sites in southwest Oregon; its objective was to test trends observed

in the GG study. Four-year results of the DFSR study are presented, relating recovery to seedling size before logging.

Grub Gulch Study

Study Area and Methods

The GG study was begun in 1980 on a north-facing, 65 percent slope, cutting unit in the Siskiyou Mountains near Medford, Oregon. The site was on land managed by the U.S. Department of Interior, Bureau of Land Management. Ranging between 900 and 1140 m in elevation, the area is considered to be site class IV (McArdle *et al.* 1961) and to have a Douglas-fir/dwarf Oregon grape (*Berberis nervosa*) plant association (Atzet and Wheeler 1984). Average annual precipitation in the area is 889 mm (Froehlich *et al.* 1982), with less than 127 mm typically falling between May and September (McNabb *et al.* 1982). The area had been skyline- and tractor-logged in 1977 as part of the preparatory/seed cut in a 2-stage shelterwood system. Understory reproduction at the time of overstory removal was a combination of natural and planted Douglas-fir seedlings. The shelterwood overstory was removed in July and August of 1980 by logging with a running skyline system using a slackpulling carriage for lateral yarding (Tesch *et al.* 1986a).

Classification of Seedling Damage After Logging. Before overstory removal, a 4.3- by 4.3-m grid was established over the entire area to be logged. Each intersection point on this grid marked the center of a 1-m-radius circular plot. If more than one seedling was present in a plot, the one with the best appearance was selected and tagged for future observation. All sample plots were revisited after overstory removal to determine the amount of seedling injury or mortality resulting from logging. Surviving seedlings were assigned to one of four damage classes (Table 1).

Information on seedlings that were killed during logging has been reported elsewhere (Lysne *et al.* 1982, Tesch *et al.* 1986b) and is not included in this article.

Classification of Seedling Recovery. In April 1984, 3 growing seasons after overstory removal, plots were revisited again to observe whether the damaged seedlings had recovered from injuries sustained during logging. Surviving seedlings were classified as crop or non-crop trees according to the following criteria:

Crop-tree criteria—

1. Previous damage insignificant or no longer evident; seedlings did not fit any of the following crop-tree criteria.
2. Broken terminal leader; lateral branch had assumed dominance.
3. Healed stem wound; crown healthy.
4. Healing stem wound; crown healthy.

Non-crop-tree criteria—

5. Debris pinning seedling to the ground.
6. Serious stem breakage below terminal leader, resulting in forked tree.
7. General lack of vigor, as shown by chlorotic needles or declining height growth.
8. Serious sweep in stem, likely to produce unstable tree.

TABLE 1. Classification of seedling damage after shelterwood overstory removal in the Grub Gulch and Douglas-fir Seedling Recovery studies.

Grub Gulch study—damage classification	Douglas-fir Seedling Recovery study—damage classification
1. No visible damage.	1. No visible damage.
2. Slight damage; broken terminal leader or small stem wound.	2. Top damaged—broken terminal leader.
	3. Stem breakage below terminal leader.
3. Moderate damage; seedlings broken off below terminal leader or stem wound covering up to half of seedling circumference.	4. Stem wound.
	5. Tree pushed to ground but not pinned by debris (free to grow); probable root damage.
4. Severe damage; usually pushed over during logging, often half the branches missing or with large portion of stem wounded.	6. Tree pinned to ground by logging slash.
	7. Lateral branches missing.
	8. Tree chlorotic; poor vigor with no obvious damage.

Evaluation of crop-tree status was based on current appearance; no consideration was given to competitive position because that could be altered by silvicultural treatments. We assumed stem damage on released Douglas-fir regeneration would not lead to significant decay if wounds healed within 10 years (Gravelle 1977). Stain and decay losses are usually negligible in trees less than 2-3 cm dbh because rapid healing compartmentalizes any defect to the wood present at the time of wounding (J. Hadfield, Forest Pest Management, USDA Forest Service, R-6, pers. comm.). We also assumed that minor flaws in tree form as a result of lateral branches expressing dominance would not lead to a significant decrease in wood quality.

Finally, we measured annual height growth for the 3-year period by observing internodal growth on either the terminal leader or on lateral branches that assumed dominance after breakage of the leader.

Statistical Analyses. T-tests were conducted to compare annual seedling growth among the GG damage classification criteria. Because plots were not replicated, ANOVA with multiple comparisons was not done. Differences between means were compared using t-tests with a 0.05 probability level.

Results and Discussion

Crop-Tree Classification and Mortality. The damage survey conducted in 1980 immediately after logging showed that the smallest seedlings had suffered the most mortality (Tesch *et al.* 1986a, b), but that surviving small seedlings had relatively few visible injuries (Table 2). The amount of moderate and severe damage increased with seedling size.

Three growing seasons after logging, the proportion of seedlings that had survived logging and that could be classified as crop trees was lowest in the 0- to 20-cm pre-harvest height class (55%) (Figure 1), the class in which surviving seedlings had the least visible damage immediately after logging. The proportion of crop trees increased through the 61- to 80-cm height class (86%), then generally leveled off.

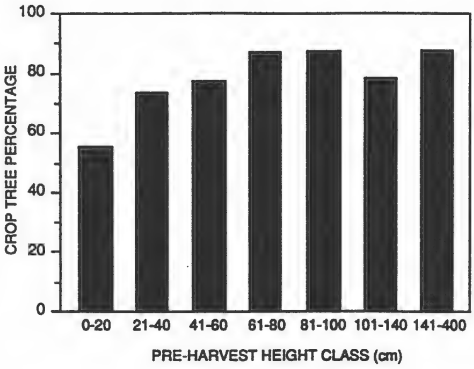

Figure 1. Percentage of Grub Gulch seedlings, by pre-harvest height class, that survived logging in 1980 and were classified as crop trees in 1984.

Of the seedlings that appeared undamaged immediately after logging, only 62 percent in the 0- to 20-cm pre-harvest height class were classified as crop trees in 1984 (Table 3), but nearly 100 percent in the 60-cm or taller pre-harvest height classes were so classified at that time. Except for seedlings in the severe damage class, the percentage that attained crop-tree status was greatest among taller individuals. Recovery of severely damaged seedlings was

TABLE 2. Seedling damage immediately after shelterwood overstory removal at Grub Gulch, by preharvest height class (n = number of seedlings in each height class).

	Preharvest height class (cm)						
Damage class	0-20 (n=82)	21-40 (n=278)	41-60 (n=187)	61-80 (n=111)	81-100 (n=79)	101-140 (n=94)	141-400 (n=65)
	% of seedlings (n) in each damage class						
None	73	61	54	40	53	22	28
Slight	11	20	19	31	22	30	34
Moderate	5	9	16	18	15	30	25
Severe	11	10	11	11	10	18	14

TABLE 3. Crop tree status of seedlings at Grub Gulch in 1984, by preharvest height class and damage class just after overstory removal (n = number of seedlings in each height class).

1980 damage class just after logging & 1984 crop-tree status	Preharvest height class (cm)						
	0-20	21-40	41-60	61-80	81-100	101-140	141-400
	% of seedlings (n) in each damage class						
No damage	(n=60)	(n=168)	(n=101)	(n=45)	(n=42)	(n=21)	(n=18)
Crop tree	62	84	92	98	100	100	100
Dead	28	8	5	0	0	0	0
Non-crop tree	10	8	3	2	0	0	0
Slight damage	(n=9)	(n=56)	(n=36)	(n=34)	(n=17)	(n=28)	(n=22)
Crop tree	56	75	78	91	82	100	100
Dead	11	12	14	9	6	0	0
Non-crop tree	33	12	8	0	12	0	0
Moderate damage	(n=4)	(n=26)	(n=29)	(n=20)	(n=12)	(n=28)	(n=16)
Crop tree	50	58	48	75	75	71	81
Dead	25	31	17	5	8	4	12
Non-crop tree	25	12	34	20	17	25	6
Severe damage	(n=9)	(n=27)	(n=21)	(n=12)	(n=8)	(n=17)	(n=9)
Crop tree	11	18	43	42	38	18	33
Dead	56	59	24	42	25	12	11
Non-crop tree	33	22	33	17	38	71	56

greatest in the 40- to 100-cm height classes; in each of these, approximately 40 percent were considered crop trees in our judgment.

By 1984, there was some mortality among seedlings in all four damage classes and in each class some survivors could not be classified as crop trees (Table 3). Of the seedlings that appeared undamaged when examined immediately after overstory removal, 28 percent in the 0-to 20-cm height class died between 1980 and 1984. Within this undamaged class, most seedlings recorded as non-crop trees in 1984 were originally 40 cm tall or less. The percentage of non-crop trees in larger size classes increased with the level of logging damage, perhaps because the damage resulted in more unacceptable tree form in these size classes.

Height Growth of Recovering Seedlings. Except for those classified as non-crop trees because of poor vigor, seedlings that survived overstory removal clearly showed accelerated height growth over the 3-year period (Table 4). Generally, undamaged trees with poor vigor were chlorotic, lacked vigorous dark green color, had small buds, and had declined in growth since logging. In the third year, average growth of crop trees was more than twice that of non-crop trees. In that year, height growth did not differ significantly among seedlings meeting the various crop tree criteria; seedlings that recovered from terminal leader or stem damage grew at the same rate as those without these injuries.

After the 1983 growing season, no growth differences were observed among crop trees originally classified as having no, slight, or moderate damage, but all of these trees had significantly greater growth than did those originally classified as severely damaged (Table 5). Crop trees that were growing vigorously and had healthy crowns when sampled after the 1983 growing season had received a wide range of logging injuries in 1980. For example, breakage of a lateral branch was recorded as slight damage in 1980, but it may no longer have been visible after 3 growing seasons. A few seedlings classified as severely damaged after logging in 1980 also showed no evidence of injury after the 1983 growing season. Some trees pinned to the ground during logging may have been uncovered and returned to an upright position after logging debris decomposed

TABLE 4. Mean annual height growth of surviving seedlings at Grub Gulch by criteria for crop and non-crop trees (±S.E.).[1]

Crop-tree & non-crop-tree criteria in 1984	Mean annual height growth (cm)			
	1981	1982	1983	n[2]
Crop trees				
Insignificant damage	12.0 (0.4)a	16.2 (0.5)a	22.2 (0.7)a	374
Broken terminal leader (healed)	8.7 (0.7)bc	15.7 (1.0)a	20.8 (1.2)a	86
Stem wound (healed)	11.9 (0.6)ab	16.1 (0.9)a	22.4 (0.9)a	173
Stem wound (not healed)	13.6 (1.8)ab	18.1 (1.9)a	29.2 (3.3)a	8
Mean, all crop trees	11.5 (0.3)	16.1 (0.4)	22.1 (0.5)	641
Non-crop trees				
Seedling pinned to ground by debris	6.4 (0.6)cd	8.6 (0.8)b	11.0 (0.8)b	42
Stem broken below terminal leader	7.3 (1.0)cd	9.3 (0.9)b	12.5 (1.8)b	13
Lack of vigor	5.1 (0.9)d	5.0 (1.0)b	5.4 (0.9)b	16
Extreme stem sweep	6.8 (1.0)cd	6.6 (0.8)b	9.9 (1.6)b	10
Mean, all non-crop trees	6.4 (0.4)	7.8 (0.5)	10.1 (0.6)	81

[1]In each data column, means identified by the same letter are not significantly different from one another at the 5 percent level according to t-tests.

[2]Number of trees with a single type of damage only; individuals with multiple injuries are deleted.

TABLE 5. Mean annual height growth of crop-tree seedlings at Grub Gulch by damage class just after overstory removal in 1980 (±S.E.).[1] (n = number of trees in each damage class.)

Damage class	Mean annual height growth (cm)			
	1981	1982	1983	n
None	11.6 (0.4)a	15.6 (0.5)a	21.6 (0.6)a	389
Slight	12.0 (0.6)a	16.6 (0.8)a	23.2 (1.0)a	157
Moderate	11.2 (1.0)ab	18.2 (1.3)a	24.6 (1.4)a	73
Severe	8.4 (1.3)b	15.3 (3.9)a	16.6 (2.2)b	22

[1]In each data column, means identified by the same letter are not significantly different from one another at the 5 percent level according to t-tests.

or moved down the slope. Most stem wounds on these relatively small trees had healed within 3 years.

Summary

Observations at Grub Gulch suggest that seedlings at least 60 cm tall are best at recovering from logging damage and becoming crop trees; 75 percent or more recovered from slight or moderate injuries. Seedlings less than 20 cm tall appear to be at greatest risk, regardless of whether damage is visible immediately after logging. Logging damage did not appear to retard height growth of trees unless they were partially uprooted or pinned down by slash throughout the observation period.

Rate of recovery from logging damage is undoubtedly a function of the environment. This site is on a northerly aspect and is characterized by Atzet and Wheeler (1984) as having the most productive plant association in the "dry end" of the Douglas-fir series. During the 3 years after overstory removal, precipitation was normal to slightly above normal, with 1983 the wettest year. At the time of remeasurement, reconnaissance

indicated a fairly dense cover of herbaceous vegetation and scattered deciduous shrubs which were typically less than a meter tall. Numerous seedlings were found within clumps of regeneration and undoubtedly suffered somewhat from interspecific competition.

Douglas-fir Seedling Recovery Study

Study Area and Methods

The DFSR study was designed to observe recovery of Douglas-fir reproduction (up to 4.6 m tall) damaged by logging on hot, dry sites in southwestern Oregon. Between September 1983 and April 1984, overstory removal was completed on 6 Bureau of Land Management timber sales in the Siskiyou and Cascade Mountains near Medford, Oregon (Table 6). All sites were logged similarly with skyline systems using slackpulling carriages for lateral yarding. Understory reproduction was a mixture of planted and natural seedlings.

During early summer of 1984, 15 permanent transects were installed within the 6 timber sales and 539 seedlings were selected for long-term observation; 92 were not visibly damaged and were selected as controls. The remaining 447 were assigned to one of eight damage categories (Table 1), and detailed measurements and damage characteristics were recorded to aid in tracking recovery over time. Most damage occurred as stem wounds, broken tops, or seedlings pushed to the ground during logging. All transects have been monitored annually so that mortality and recovery could be related to seedling size and type of injury at the time of overstory removal. Fourth-year results are presented here. Data on growth and crop-tree status will be collected after 5 years and are not yet available.

Results and Discussion

In the long-term DFSR study, cumulative mortality after the 1987 growing season (4 years after overstory removal) was greatest for those seedlings that had been 0- to 30-cm tall right after logging; among them, mortality rate was about 40 percent for both damaged and undamaged seedlings (Figure 2). Nearly two-thirds of the mortality of damaged seedlings in this smallest size class occurred in the first growing season, and almost all mortality had occurred by the end of the second. Most of the damaged seedlings that died had been pinned to the ground or pushed over. Stem wounds, broken terminal leaders, or missing lateral branches did not commonly lead to mortality. Mortality of undamaged seedlings in this size class occurred throughout the 4-year period.

TABLE 6. Site descriptions for Douglas-fir Seedling Recovery study.

Site	Number of transects	Percent slope	Aspect	Elevation (m)	Precipitation (mm)		Plant association[3]	Mountain range
					Annual[1]	Dry season[2]		
1	1	50	W	1010	864	114	Douglas-fir - ponderosa pine	Siskiyou
2	5	25-50	N,NE,S	775	1041	135	Douglas-fir - white fir/ ocean spray; Douglas-fir - depauperate	Siskiyou
3	2	40	NE	940	1270	165	Douglas-fir - jeffrey pine	Siskiyou
4	4	60	N,NW,S	850	860	120	Douglas-fir - white fir/ ocean spray	Siskiyou
5	1	60	W	1070	1270	160	Douglas-fir/ dwarf Oregon grape	Cascade
6	2	65	SE	700	1270	160	Douglas-fir/ poison oak - Piper's Oregon grape	Cascade

[1]Source: Froehlich *et al.* 1982.
[2]Source: McNabb *et al.* 1982. Dry season = May through September.
[3]Source: Atzet and Wheeler 1984.

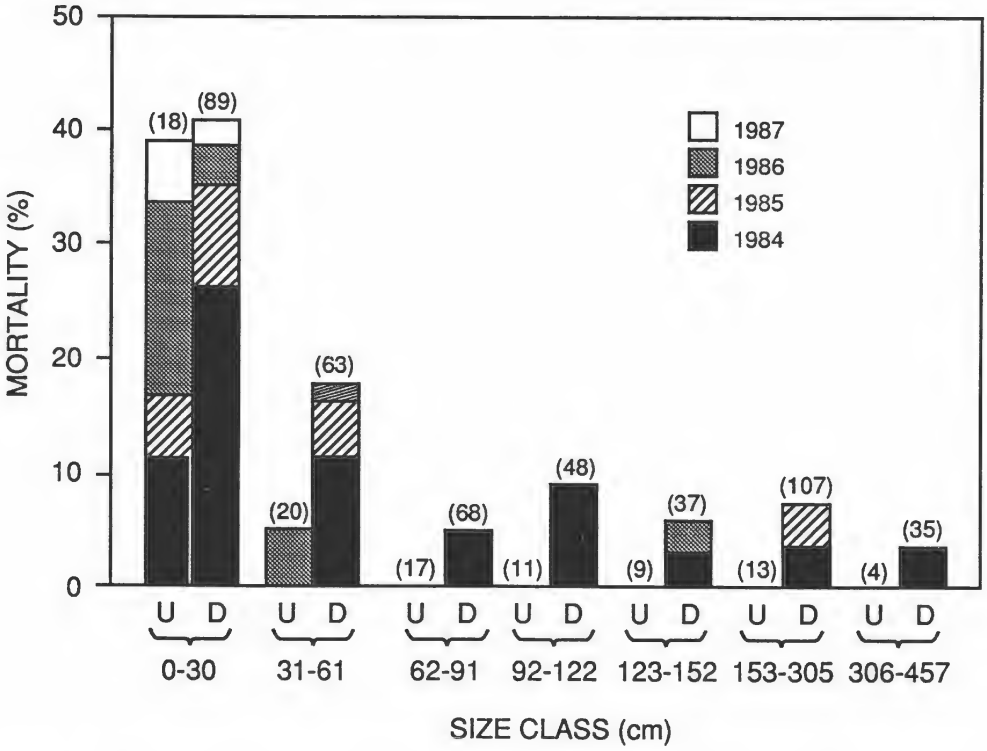

Figure 2. Mortality of undamaged (U) and damaged (D) trees on transects installed in 1984 as part of the DFSR study. Numbers above bars represent initial numbers of seedlings in each column. Data from all transects have been pooled.

At the end of 1987, cumulative mortality of damaged seedlings in the 31- to 61-cm size class was 17 percent, less than half that of corresponding seedlings in the smaller size class. As with the smaller class, most mortality occurred in the first 2 years after logging. Mortality of damaged trees in larger size classes was less than 10 percent, most of which occurred in the first year. Only a small number of undamaged seedlings greater than 30 cm tall suffered mortality. While survival of larger, damaged seedlings has been good, crop-tree status is not yet available.

We were intrigued that mortality of apparently undamaged 0- to 30-cm tall seedlings continued throughout the 4-year period, especially in the third year (1986), even though mortality of damaged seedlings of similar size was low after the first 2 years. Mortality in 1986 for apparently undamaged seedlings was 17 percent compared to only 3 percent for damaged seedlings. Adverse environmental conditions or competition are likely causes for mortality of these small seedlings, but we were surprised that mortality was not more similar between the two groups in 1986. The fact that many damaged seedlings died quickly in the first 2 years would not seem to preclude susceptibility of remaining seedlings to environmental- or competition-related mortality. Typically, mortality declines over time as seedlings become established, unless some other factor is weakening them. We offer an alternative hypothesis that when logs roll over small, flexible seedlings, invisible root and stem damage may occur that predisposes seedlings to mortality over time. While we have no direct evidence to support this hypothesis, we feel further study is warranted because of the common notion that very small flexible seedlings suffer less logging damage.

Summary

The key finding to date from this study is that seedlings larger than about 60 cm tall suffered the least mortality after being damaged during logging. While crop-tree status has not been determined, 90 percent of damaged trees above this size are alive after 4 years. Most mortality is related to seedlings being partially uprooted or pinned to the ground.

The transects are all located on sites judged to be at least moderately hot and dry (Atzet and Wheeler 1984), thereby making competing vegetation a potentially important influence on recovery. Competing vegetation was not controlled in any of the harvest areas and reconnaissance indicated that herbaceous plants rapidly occupied the transects after overstory removal. Shrubs and hardwood sprouts are beginning to dominate most sites after 4 years. Precipitation during the recovery period has been normal to below normal, with annual precipitation for 2 years at least 20 percent less than normal.

Synthesis and Conclusions

Evaluation of crop-tree status at Grub Gulch demonstrated that Douglas-fir seedlings damaged during shelterwood overstory removal can recover within 3 years. Even among seedlings originally classified as severely damaged, nearly 40 percent of those between 41 and 100 cm tall were judged to be crop trees 3 years later. Recovery of less severely damaged trees was much better. Only among severely damaged seedlings was annual height growth significantly reduced 3 years after harvest.

In both studies, damaged seedlings in the smallest size classes (less than 31 cm tall) suffered the greatest mortality. Of those that survived, many at Grub Gulch were not judged to be crop trees at the end of the observation period.

For both studies, nearly 40 percent of the undamaged seedlings in the smallest size classes either died or, in the case of Grub Gulch, were classified as non-crop trees. While poor planting, competition, and adverse environmental conditions are likely the main causes, some invisible damage to roots and stems of these highly flexible seedlings is hypothesized.

Survival and recovery of damaged Douglas-fir seedlings in both studies were much higher when seedlings were at least 40 to 60 cm tall at the time of overstory removal. This limited evidence might encourage timber sale planners to consider scheduling shelterwood overstory removal when Douglas-fir reproduction, planted seedlings in particular, is at least 40 cm tall.

These studies document that understory reproduction can recover from substantial logging-related injuries. Our database is limited at this time and caution should be exercised in extrapolating our results, but it does appear that a classification system based on damage incurred during logging can be developed and become a useful tool in predicting subsequent recovery.

Acknowledgments

These studies were conducted as cooperative research projects between Oregon State University's Southwest Oregon Forestry Intensified Research Program (FIR) and the Bureau of Land Management, Medford District. FIR, established in October 1978, is a cooperative effort involving Oregon State University, the Bureau of Land Management, the USDA Forest Service, and southwest Oregon counties and timber industries. It is designed to help foresters and other specialists solve complex biological and management problems important to southwest Oregon, and represents a determined effort by the southwest Oregon forestry community and county governments to find practical solutions to those problems. This is paper 2389, Forest Research Laboratory, Oregon State University, Corvallis.

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Received 23 March 1988
Accepted for publication 10 December 1989

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Frost Distribution and Occurrence on a Rangeland Watershed in Southwest Idaho*

Abstract

In the Pacific Northwest, one of the primary causes of severe flooding and soil erosion is rain and/or snowmelt on frozen soil. This study gives a descriptive view of how location on a watershed and the associated antecedent soil water (fall precipitation), air temperature, and snow cover affect depth and occurrence of soil frost. Hydrologic and climatic data from three sites on the Reynolds Creek Experimental Watershed in southwestern Idaho for the 1976 through 1984 winter seasons were used in the study. Maximum seasonal frost depths averaged 42 cm at the lowest elevation site where fall precipitation was the least and snow cover at the time of maximum frost depth averaged only 1 cm. At the mid and highest elevation sites, the maximum seasonal frost depths averaged 26 and 24 cm, respectively. Snow cover averaged 9 and 44 cm at the time of maximum frost depth at the upper two sites. Air temperatures at the higher elevations were colder and remained colder longer than at the lower elevation sites; however, frost penetration at the high elevations was less because of deeper snow cover and more fall precipitation. When soil frost occurred at the high elevation site, it stayed longer than at the low elevation site where there was more than one freeze-thaw cycle during several seasons. In general, the low elevation site had the deepest maximum soil frost depth because of dry soil conditions, lack of snow cover, and cold night temperatures. Because of snow cover and warmer night time temperatures at the mid elevation site, average maximum soil frost depth at the mid and high elevation sites was about the same which was a little more than one-half of the average maximum frost depth at the low elevation site.

Introduction

Flooding and soil erosion from runoff often result when rain and/or snowmelt occurs on frozen soil. Loss of soil and associated reduced productivity are two reasons for studying soil frost. These losses can have considerable impact on the management practices in frost-prone areas.

The occurrence of soil frost depends upon a complex mix of site characteristics and climatic factors. Magnitude and duration of subfreezing air temperatures, soil water, snow depth, soil type, and vegetation cover, as well as slope and aspect, have a significant influence on the rate of frost penetration, frost depth and areal extent, and type of soil frost.

Several investigators have reported that dry soils freeze deeper and faster than wet soils (Willis *et al.* 1961; Steppuhn 1981). They also reported that dry soils thawed faster than wet soils.

Benoit (1973) pointed out that in soils with a high moisture content, soil hydraulic conductivity may decrease due to freezing and thawing regardless of soil aggregate size or freezing temperature, but soil with a low water content will do just the opposite. However, Hinman and Bisal (1973) showed that freezing and thawing tend to increase the hydraulic conductivity of high water content clays and reduce the conductivity in loam soils. Alternating freezing and thawing tended to reduce the conductivity less in loam soils than a continuous freeze.

Previous studies indicate that next to air temperature, snow cover probably has the greatest effect on frost penetration. Bullard (1954) summarized observations made by others in previous studies. He reported that snow depth was controlled by plant cover, aspect, and local topography, and that density of snow affects its insulating ability. One study showed that with a snow depth of at least 90 cm, there was sufficient insulation to prevent soil freezing. Soil that is initially frozen began to thaw with a snow cover of at least 25 cm. It was reported that for each 10 cm of snow, frost depth was reduced by 80

*This paper is a contribution from the Northwest Watershed Research Center, USDA-ARS, Boise, Idaho and University of Idaho, Agricultural Experiment Station, Moscow, Idaho.

percent. Steppuhn (1981) reported, that in Europe, a rule-of-thumb is that for every centimeter of snow cover, soil temperature in the root zone increases by at least 0.1°C. Hale (1950; 1951) reported that up to 19 cm of impermeable frost occurred in sagebrush and grass ranges in eastern Oregon and Washington during winter and spring snowmelt. Over 13 cm of concrete frost thawed under about 25 cm of snow cover, and with a snow depth of 76 cm on east slopes frost disappeared.

Bay *et al.* (1952) showed that 46 cm of snow insulated the soil sufficiently to prevent frost penetration past a depth of 30 cm when the average daily minimum temperature was as low as —25°C. The 46 cm of snow did not prevent frost penetration past the same depth when the average daily minimum temperature was —29°C; however, frost penetration was stopped when the snow depth was increased to 61 cm. Winters with little snow permitted frost penetration to as much as 91 cm under usual farming practices.

The purpose of this paper is to give hydrologists and others interested in mountainous environments a descriptive view of the temporal and spatial distribution of soil frost in watersheds that are located within mountain ranges. To accomplish this goal, hydrologic and climatic data from three weather station sites on the Reynolds Creek Experimental Watershed in southwestern Idaho were used to illustrate how location on the watershed and associated antecedent soil water (fall precipitation), air temperature, and snow cover affect depth and occurrence of soil frost.

Methods

Watershed Description

The Reynolds Creek Experimental Watershed (Figure 1) has been operated by the U.S. Department of Agriculture, Agricultural Research Service (ARS), Boise, Idaho since 1960 for the purpose of studying water yield, flood flow, sedimentation, and range resources (Robins *et al.* 1965). The stream is a foothill tributary of the Snake River and is located approximately 64 km southwest of Boise, Idaho.

The 234 km^2 watershed is approximately 29 km long and from 4.8 to 11.3 km wide. The valley is the deepest declivity in the rolling plateau country between the Snake River and the Idaho-Oregon border. The valley floor has an elevation of about 1,160 m a.s.l., while the surrounding rim averages about 1,830 m elevation. The highest peak in the watershed is about 2,100 m elevation with isolated peaks to the south and west of the valley rising to 2,400 m (Cooper 1967). The north and northwest trending ridges with gently inclined windward slopes and steep north and east facing slopes are vegetated with sagebrush (*Artemisia* spp.) and other rangeland grasses. Intermittent stands of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), western juniper (*Juniperus occidentalis* Hook.), aspen (*Populus tremuloides* Michx.), and scattered meadows occur in the higher elevations. These areas comprise only about 2 percent of the total watershed and are found mainly in protected or snow drift areas in the higher elevations. About 610 ha of irrigated hay are grown in the valley along the lower reaches of the main channel and its tributaries (Hamon and Johnson 1965). While the vegetation in the watershed is principally sagebrush and related woody species, there is an understory of annual or perennial grasses.

Winter precipitation varies with elevation as well as with location on the watershed with the leeward sites receiving more precipitation than windward sites at equal elevations (Hanson *et al.* 1980, Hanson 1982). The location of maximum annual precipitation on the watershed is just leeward of the western watershed boundary. Annual precipitation varies from about 250 mm at the lower elevations to 1,150 mm at the higher elevations. About 80 percent of the annual precipitation occurs from October through April and is mainly in the form of snow at the high elevations. At the lower elevations, about 67 percent falls during the same period and is about 25 percent snow. This precipitation is a result of general frontal-type storms moving in from the west-southwest (Molnau *et al.* 1980; Hanson *et al.* 1980). Snowfall on the watershed is strongly influenced by a predominantly southwest wind interacting with vegetation and local topography so that snow is deposited in irregular spatial patterns. Under some circumstances, a considerable amount of the snowfall is concentrated by wind within a small area of the watershed (Rawls and Jackson 1979).

Watershed soils are predominantly residual, having been developed from volcanic rock, granite, and lake sediment parent material (Stephenson 1977) (Table 1).

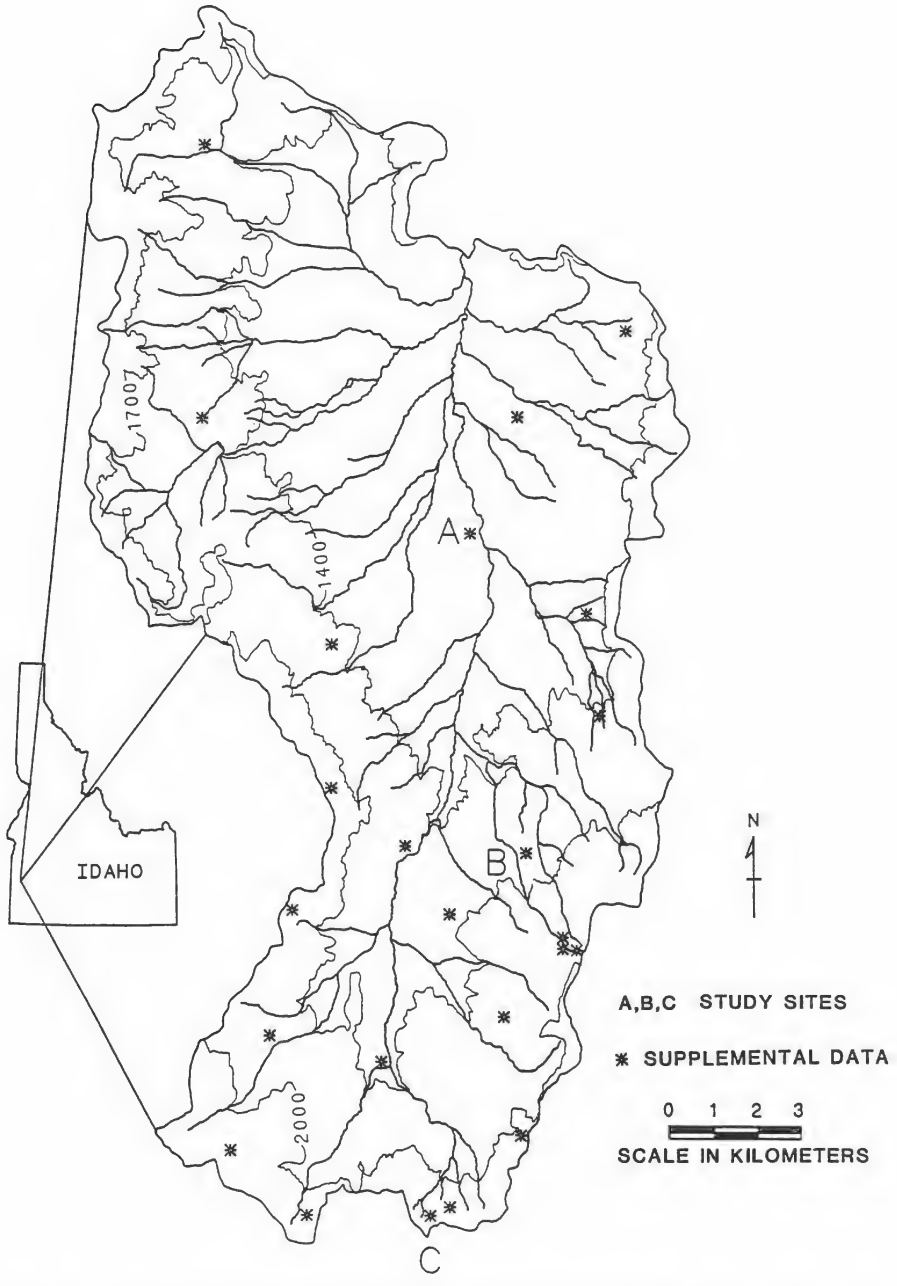

Figure 1. Vicinity map, topography and frost sites of the Reynolds Creek Experimental Watershed, Idaho. Depth of frozen soil was measured by soil water resistance blocks and frost tubes at sites A, B and C and only by soil water resistance blocks at the other sites.

TABLE 1. Description of soils at frost study sites on Reynolds Creek Experimental Watershed, Idaho.

Site	Elevation (m a.s.l.)	Aspect	Geologic Material	Soils					Vegetation
				Subgroup	Family	Series	Field Capacity (g/g)	Wilting Point (g/g)	
A	1193	Flat	Sedimentary	*Xerollic Haplargids*	Fine loamy, mixed, mesic	Larimer stony loam	27	14	Big sagebrush-grass
B	1649	N	Basalt	*Calcic Argixerolls*	Loamy skeletal, mixed, frigid	Searla gravelly loam	29	14	Low sagebrush-grass
C	2097	NW	Rhyolite	*Pachic Cryoborolls*	Fine loamy, mixed	Bullrey gravelly loam	25	9	Big sagebrush-grass

Soil Frost Measurements

Frost penetration data for 1976 through 1984 for three sites (A, B, and C) (Figure 1) were used in this study. These data were measured using soil water resistance blocks (Burgess and Hanson 1979) and frost tubes. Two sets of resistance blocks were installed at a level site at each location. The blocks were positioned at 5, 10, 15, 20, and 30 cm depths. In addition, one stack of blocks at site A was positioned at 5, 10, 15, 20, 30, 40, 50, and 60 cm depths. Frost depth was measured on a weekly basis during the cold period at sites B and C, and more often at site A. Frost penetration was known to be somewhere between two adjacent depths, e.g., frozen at 5 cm but not at 10 cm. When soil frost was measured at 30 cm, the depth was noted as 30 cm or greater.

Several investigators (Garstka 1944; Harrold and Roberts 1960; Sartz 1967) have shown soil water blocks to be reliable and easy to use. Burgess and Hanson (1979) reported that frozen soil conditions could be accurately determined using soil-water blocks. The changes in electrical resistivity of the material in the blocks caused by freezing and thawing were measured. A sharp rise in resistance indicated soil freezing while a drop in resistance indicated soil thawing.

Frost tubes filled with sand and dye solution were used along with the frost blocks. These frost tube type gages are similar to those described by Harris (1970). The tubes were installed to a depth of 100 cm in the soil and protruded above the ground surface. When the soil temperature was below freezing, the dye solution within the tubes changed color, indicating the presence of a below freezing temperature, and presumably frost. Harris (1970) reported that the tube-type gage is economical and is a reliable indicator of frost depth to within plus or minus 5 cm of the indicated true frost depth, 95 percent of the time.

Where frost data were missing, depth of frost and snow was interpreted by comparing frost and snow depth at other sites with a similar local environment. Frost depth was the maximum indicated by either method previously described; however, most frost data reported herein were from frost tubes. This study was concerned with frost depth only; any surface thaw that may have occurred while a portion of the soil profile was frozen was not included.

Daily maximum and minimum air temperatures were measured by hygro-thermographs at the three sites. Snow depth was measured at the time of frost readings and it represented average depth at the site of frost measurement. Precipitation was measured by a dual-gage system located at each frost site (Hamon 1973; Hanson *et al.* 1980). The dual-gage system consisted of an unshielded and a shielded gage and the amount of precipitation was computed from a logarithmic relationship which used the catch in both gages. This system has proven to provide reliable measurements of both rainfall and snowfall (Hamon 1973; Hanson *et al.* 1980).

Results and Discussion

The years chosen to illustrate the effect of site location on frost depths were 1977-78, 1978-79, and 1983-84 because each of these years was quite different from the other. Soil frost depths for 1976-77 through 1983-84 frost season, long-term mean monthly temperatures, and the mean monthly temperatures for the selected years are listed in Tables 2 and 3. Precipitation during the fall of 1977-78 was about average with a shallow snow cover (Table 2), and the midwinter temperatures were about 2°C above average (Table 3). During the fall of 1978-79, precipitation was between 13 and 60 mm below average with moderate snow cover and winter temperatures that were about 4°C below average (Table 3). Precipitation during the fall of 1983-84 varied between 14 and 25 mm below average (Table 2) with deep snow cover and winter temperatures that were about 2°C below average (Table 3).

Frost and snow depths at the three sites are shown in Figures 2-4 and monthly temperatures are shown in Table 3. Frost penetration at site A was as great or greater than at sites B or C for all but site C during 1977-78. This manifestation of persistent frost depth is also shown in the summary in Table 2. The maximum frost depths noted at site A for the years 1977-78, 1978-79, and 1983-84 were 14, 80, and 39 cm, respectively (Table 2). For the same periods, the frost depths were 13, 80, and 18 cm for site B and 22, 46, and 0 cm for site C. Occasionally, initial frost at site C occurred at the same time of year or preceded the initial frost at site A. For example, during 1978-79 initial frost occurred at both sites on 13 November 1978.

Site A also experienced considerably shorter frost durations relative to other sites at higher

TABLE 2. Occurrence of soil frost at sites A, B and C on Reynolds Creek Experimental Watershed, Idaho, 1976-1984.

Site	Year	Fall Precipitation Sept-Nov (mm)	Maximum Frost Depth			Occurrence of Frost	
			Depth (cm)	Date	Snow Cover (cm)	First (date)	Last (date)
A	1976-77	43	58	01 14 77	5	11 29 76	02 14 77
	1977-78	68	14	11 21 77	2	11 18 77	01 06 78
	1978-79	44	80	02 07 79	0	11 13 78	02 16 79
	1979-80	42	42	02 04 80	0	11 20 79	02 19 80
	1980-81	96	45	12 22 80	0	11 17 80	02 17 81
	1981-82	73	45	02 17 82	0	01 11 82	02 18 82
	1982-83	71	15	11 26 82	2	11 26 82	02 15 83
	1983-84	78	39	01 25 84	0	12 16 83	03 05 84
	Average	64	42		1	11 30	02 13
B	1976-77	48	32	01 31 77	0	12 28 76	02 09 77
	1977-78	62	13	11 22 77	18	11 22 77	03 21 78
	1978-79	63	80	02 06 79	8	11 14 78	03 13 79
	1979-80	55	25	02 05 80	0	11 13 79	03 03 80
	1980-81	85	17	01 19 81	0	12 02 80	02 19 81
	1981-82	86	9	02 10 82	38	01 06 82	02 17 82
	1982-83	107	17	12 14 82	8	12 07 82	02 23 83
	1983-84	101	18	02 07 84	0	12 27 83	03 13 84
	Average	76	26		9	12 07	03 01
C	1976-77	84	55	02 14 77	15	12 06 76	04 06 77
	1977-78	208	22	12 28 77	23	11 10 77	03 13 78
	1978-79	117	46	01 09 79	76	11 13 78	03 26 79
	1979-80	159	24	01 15 80	46	11 27 79	04 22 80
	1980-81	163	21	01 20 81	0	11 24 80	03 17 81
	1981-82	218	22	02 16 82	61	01 13 82	04 27 82
	1982-83	261	6	01 04 83	91	11 22 82	02 15 83
	1983-84	197	0	02 23 84	122[1]	—	—
	Average	176	24		54	11 29	03 27

[1]Depth given to indicate snow cover only.

TABLE 3. Average and seasonal air temperatures at sites A, B and C on Reynolds Creek Experimental Watershed, Idaho.

Site	Oct	Nov	Dec	Jan	Feb	Mar	Apr
			Average Daily (°C)				
A (1964-84)	8	3	−1	−2	2	3	6
1977-78	9	4	3	2	3	7	7
1978-79	10	2	−4	−7	1	3	6
1983-84	10	4	−4	−4	−1	4	6
B (1967-84)	8	2	−2	−3	0	2	4
1977-78	10	1	0	0	0	6	5
1978-79	11	1	−5	−8	−1	2	4
1983-84	10	2	−5	−4	−2	2	3
C (1967-84)	5	−1	−5	−5	−3	−3	0
1977-78	7	−1	−3	−2	−2	3	1
1978-79	9	−2	−9	−9	−5	−2	−1
1983-84	7	−2	−7	−3	−3	−1	0
			Average Daily Maximum (°C)				
A	16	8	3	3	7	9	13
1977-78	17	9	7	6	7	14	12
1978-79	19	8	1	−2	5	10	13
1983-84	17	8	0	1	3	10	12
B	12	5	1	0	4	5	9
1977-78	14	5	3	2	2	9	9
1978-79	16	4	−2	−5	1	6	9
1983-84	14	5	−2	0	2	5	8
C	9	2	−2	−2	0	1	4
1977-78	11	2	−1	0	1	6	4
1978-79	13	1	−5	−7	−3	1	3
1983-84	12	1	−4	2	2	4	5
			Average Daily Minimum (°C)				
A	1	−3	−6	−6	−3	−3	−1
1977-78	1	−2	−2	−2	−1	0	1
1978-79	1	−4	−9	−13	−3	−3	−1
1983-84	2	0	−8	−8	−4	−1	0
B	4	−2	−5	−6	−3	−2	0
1977-78	5	−2	−3	−2	−2	2	1
1978-79	6	−2	−8	−11	−3	−2	0
1983-84	6	−1	−8	−7	−5	−1	−1
C	1	−4	−7	−8	−6	−6	−4
1977-78	3	−4	−5	−4	−5	−1	−2
1978-79	4	−5	−12	−12	−7	−5	−4
1983-84	3	−4	−9	−7	−7	−5	−4

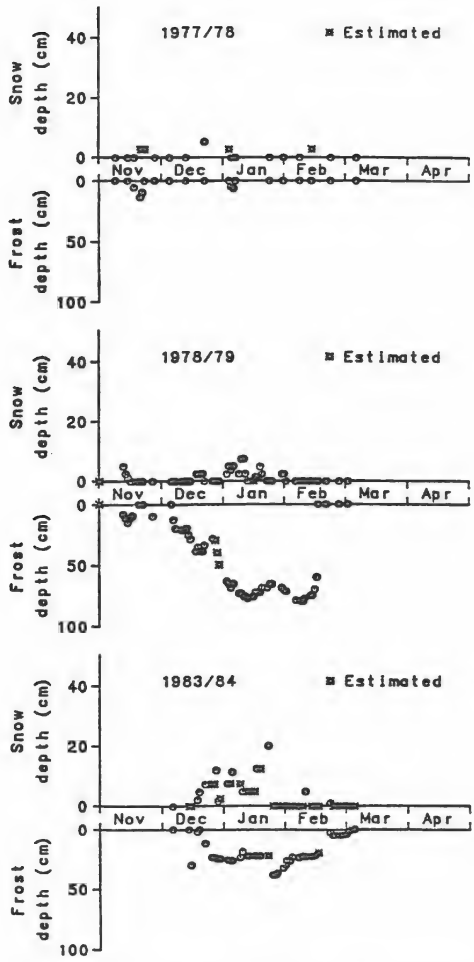

Figure 2. Frost and snow depth for three seasons at site A.

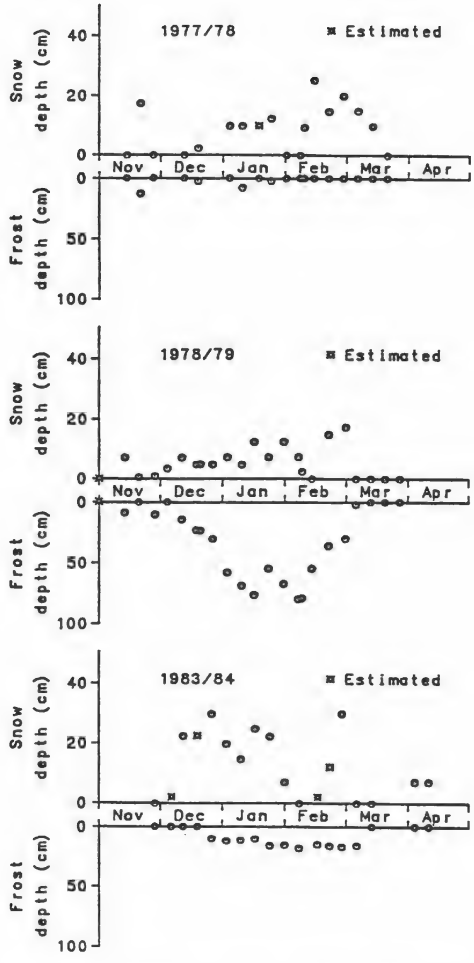

Figure 3. Frost and snow depth for three seasons at site B.

elevations. For example, during 1978-79 at site A (Figure 2), the depth of soil frost fluctuated during the season and the season was shorter than at site C (Figure 4) where the depth of frost was less and the depth did not vary much during the period of snow cover. In addition, site A typically experienced an earlier occurrence of initial frost and quicker thaw than the sites at higher elevations.

Lower elevations experienced deeper frost depths than higher elevations because there was less snow cover at the lowest elevation site and the minimum air temperatures were lower than mid elevation temperatures (Table 3). This phenomena was a result of cold air drainage.

The average monthly air temperatures at the three sites are listed in Table 3. Site A had the coldest extreme minimum temperature and about the same average monthly minimum temperature as the other sites which, along with the minimum snow cover and driest soils, resulted in the deepest frost penetration. Site A also had the overall shortest frost season because of the warmer maximum temperatures and little or no snow cover.

Site B had the overall warmest minimum temperatures and, on average, the shallowest

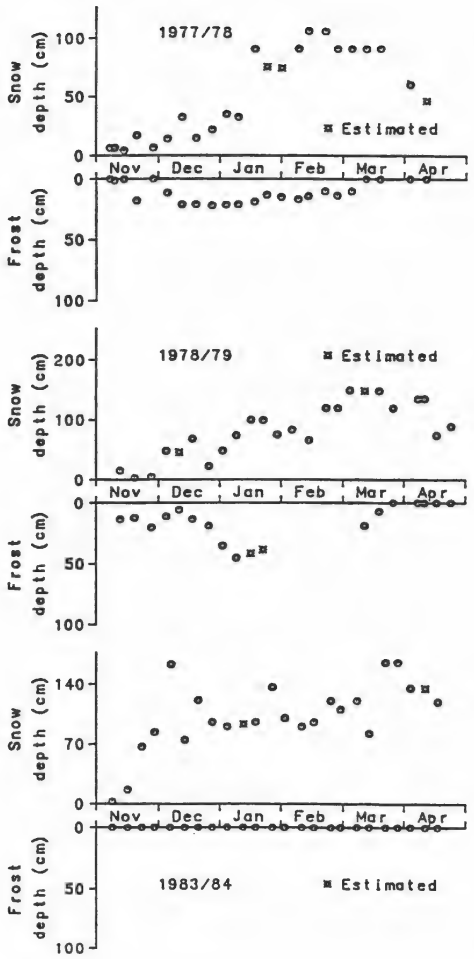

Figure 4. Frost and snow depth for three seasons at site C.

frost depth. For example, in 1976-77 the mean minimum temperature for January was —5°C with a maximum frost of 32 cm (Table 2). Sites A and C for the same period had mean minimum temperatures and maximum frost depths of —11°C and 58 cm, and —7°C and 55 cm, respectively.

Site C had the most snow cover and, generally, frost depth was less than at site A. The maximum frost depth and the amount of snow cover at time of maximum frost depth are shown in Table 2. During the years of deeper snow depths, snow provided sufficient protection to prevent soil frost which agrees with studies summarized by Bullard (1954). This insulative effect was observed at site C during the 1983-84 winter period (Figure 4). When frost with a snow cover did occur at this site, the duration of frost tended to be longer than at site A as seen in Figures 2 and 4 for 1977-78.

During the winter of 1983-84, snow began to accumulate at site C about the second week of November. As temperatures dropped with the onset of winter, the upper elevation of the watershed was protected by a snow cover before subfreezing air temperatures arrived. Snow continued to accumulate and provided insulative cover to the soil which remained unfrozen throughout the winter. The snow remained well beyond April and soil was not exposed until warmer temperatures were predominant. At the same site in 1977-78 there was little, if any, snow cover on the ground at the time when freezing began during the last week of November and first week of December. A frost depth of about 22 cm persisted into the fourth week of January when a heavy snowfall occurred. Frost remained in the soil until March 13, 1978 under a snow depth of about 1 m. At lower elevations in the watershed, the snow started to accumulate late in the fall and did not develop as deep and melted earlier in the spring than at higher elevations. Frost was generally confined to the soil where the snow was shallow. The lower elevations of the watershed were free of snow by the middle of February.

Maximum frost depth, snow depth at time of maximum frost, and the occurrence of soil frost for the three study sites are shown in Table 2. It can be seen that there is a wide variation in maximum frost depth between the three sites, again, with greater depths of frost and lesser snow cover being more noticeable at lower elevations. For example, at site A for 1978-79, the maximum frost depth was 80 cm with no snow cover. At site C the maximum frost depth was 46 cm with 76 cm of snow.

The maximum soil frost depth during 1978-79 was not only caused by a shallow snow cover and cold air temperatures, but also by dry fall soil conditions (Table 2). In general, soil frost did not penetrate as deep during winters that followed a wet fall.

Conclusions

On the Reynolds Creek Experimental Watershed, depth of maximum frost penetration and the time of maximum depth varied between seasons at each of the study sites. At the lowest elevation site (site A), the maximum seasonal frost depth varied between 14 cm on November 11, 1977 to 80 cm on February 7, 1979, with an average of 42 cm for the winter seasons of 1976-77 through 1983-84. The average seasonal maximum frost depth was greatest at site A because of the shallow snow cover which averaged only 1 cm at the time of maximum frost depth, and because the site received the least fall and winter precipitation.

The maximum seasonal frost depth at the mid elevation site (site B) varied between 9 cm on October 2, 1982 to 80 cm on February 6, 1979, with a mean maximum depth of 26 cm. In general, the maximum frost depth was less at site B than A because of deeper snow cover, more fall and winter precipitation, and warmer minimum temperatures.

The highest elevation site (site C), where there was the deepest average snow cover (54 cm) and the most fall and winter precipitation, had a 24 cm average maximum soil frost depth, which was the least of the three sites. The seasonal frost depth varied between 0 in 1983-84 to 55 cm maximum on February 14, 1977. An observed snow depth of about 1 m prevented soil frost at this site.

A combination of minimum air temperature, depth and timing of snow cover, and the amount of soil water were factors that determined the depth of soil frost at the three study sites. Soil frost depth was not uniformly distributed throughout the watershed.

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Received 22 November 1988
Accepted for publication 10 December 1989

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Recharge Estimates for the Hanford Site 200 Areas Plateau

Abstract

The magnitude of recharge from natural precipitation was assessed on the Hanford Site 200 Areas Plateau. Two sources of data were used in the evaluation: (1) moisture accumulation in an 18-m-deep 200 East Area, closed-bottom lysimeter for 13 yr, and (2) distribution of ^{137}Cs in a solid-waste burial ground in which contaminated soil had been buried for 10 yr. A borehole was core drilled in 1985 to the bottom of the 200 East Area closed-bottom lysimeter and the moisture content was determined gravimetrically. The 1985 moisture content of the lysimeter was compared with its initial moisture content to estimate the recharge. There was an apparent net loss of moisture during the 13-yr experiment. There has been no detectable moisture accumulation in the bottom of the lysimeter since 1972. Thus, the recharge rate was approximately zero over the 13-yr period (0 ± 0.2 cm/yr [2 standard deviations]). Cesium-137 contaminated soil, resulting from a multimolar, NH^{+}_{4} waste spill, was placed in a 200 West Area solid-waste burial ground in 1970. After 10 yr, the distribution of ^{137}Cs was determined from core-drilled samples. No ^{137}Cs above background was detected beneath the trench bottom. Thus, there was no indication of measurable downward movement. However, ^{137}Cs was detected above the trench, most likely resulting from evapotranspiration. Based on the above observations, there appears to be very little potential for downward movement of mixed waste contaminants in the upper vadose zone beneath much of the 200 Areas Plateau under natural or minimally disturbed conditions.

Introduction

A significant portion of the nuclear and hazardous waste inventory at the Hanford Site in Washington state is stored in the vadose zone (unsaturated zone above the water table) on the 200 Areas Plateau. The proportion of natural precipitation that percolates through the vadose zone to groundwater beneath the 200 Areas Plateau is required to assess the long-term environmental impact of Hanford Site waste storage and disposal. Infiltrating precipitation (recharge) is the transport medium that may carry a portion of this waste to the groundwater, and ultimately, to the Columbia River and the surrounding population.

The literature and data provided in this paper are limited to studies and data concerning the Hanford Site 200 Areas Plateau. There is additional literature that has been used to evaluate Hanford Site recharge processes (e.g., Gee and Kirkham 1984). However, the Gee and Kirkham (1984) data and evaluations are *not* directly applicable to recharge on the 200 Areas Plateau because of the locations from which much of the data were taken and the types of sediments studied. The above data were also collected in considerably different microclimates and from sediments that tend to be more homogeneous than the layered strata of the 200 Areas Plateau. The surface of the sites studied by PNL (Gee and Kirkham, 1984) have generally been reworked by wind, resulting in a more homogenized sediment than the laminated and finely bedded, varve-like, strongly layered sediments noted above (Fecht *et al.* 1977, Routson and Fecht, 1980). Alternating fine and coarse-textured sediments can have a profound effect on the movement of moisture through partially saturated sediments. The tendency is for layering to limit the percolation rate of precipitation and to allow added time for evapotranspiration to further limit net recharge.

Natural recharge to groundwaters results from the infiltration and redistribution of meteoric water in areas without artificial recharge (ground disposal) and surface-water sources. Percolation through sediments surrounding buried waste is the primary source for recharge from any waste-burial operation. The movement during redistribution is a continuous, cyclic process. The cycle is initiated with the infiltration of precipitation into the soil. This is followed by temporary storage and redistribution of water to deeper sediments. The final portion of the cycle is the removal of water from the sediments by evaporation, transpiration (plant withdrawal), and deep drainage (recharge) to the water table. The objective of our work was to assess the magnitude of the deep drainage portion of this cycle and the potential for downward waste migration under actual disposal site

conditions at the Hanford Site. To accomplish this objective, two principal data sources were relied upon: 1) a deep lysimeter study that has been continued for more than 13 yr (Jones 1978), and 2) radionuclide depth-distribution data from core samples taken from a solid-waste burial ground trench. Both of these sources provide relatively long-term data (13 yr and 10 yr, respectively) for this evaluation.

Study Area

The Hanford Site lies in a broad, alluvial basin located on the Columbia Plateau of eastern Washington state. The locations of the major waste management areas (200 West and 200 East) within the Hanford Site boundary, the study sites and the plateau region are shown in Figure 1. The deep lysimeter site is located adjacent to the south fenceline of the 200 East Area while the burial ground (trench) site is located within the 200 West fenceline. There is a permanent meteorological station approximately 2 km east of the burial trench site from which precipitation and evaporation data used in this study were obtained.

The 200 Areas Plateau is a broad bar of Pleistocene flood deposits roughly defined by the 700-ft (213 m) contour (i.e., elevation above mean sea level; shown as the stippled boundary in Figure 1). The vadose zone varies in thickness from approximately 61 m in the 200 West Area to 81.4 m in the 200 East Area. The plateau is generally covered with light-textured, sandy soil underlain by stratified and/or cross-bedded sands, silts and gravels. Typical textural variations in these deposits, and their influence on moisture movement, are illustrated in Figure 2. Biologically, the Hanford Site is frequently referred to as a shrub-steppe ecosystem or mid-latitude desert where the aridity arises from its geographic location in the "rain shadow" of the Cascade Mountains to the west. Average annual precipitation is 15.7 cm/yr based on a 4-yr record (Stone *et al.* 1972). The corresponding "actual evapotranspiration" as calculated by the Thornthwaite-Mather method (Thornthwaite and Mather, 1955) was estimated to be 16 cm/yr (Gutknecht *et al.* 1980). Sagebrush and cheatgrass are the dominant plants on the 200 Areas Plateau.

Methods and Materials

The lysimeter and burial ground studies are described in separate subsections of the following discussion.

Lysimeter Study

Computational Approach. Drainage can be mathematically described as a quasi-steady state in the deeper sediments. The moisture content in the deeper sediments (below about 3 m at the Hanford Site 200 Areas Plateau) tends to remain constant (Jones 1978, Last *et al.* 1976). The travel time of deep-draining moisture to some depth (below the depth to which evapotranspiration occurs), such as the water table, can be determined if the recharge rate and volumetric water content of the sediments are known (Heller *et al.* 1985). The volumetric water content is the constant volume of vadose zone water divided by the volume of soil (expressed as a percentage). The moisture content of soil below about 7 m on the 200 Areas Plateau, although slightly variable, tends to average about 6%. Dividing the recharge (cm/yr) by the volumetric water content (6%) provides the depth (distance) moisture will travel per year (the velocity). Dividing the depth to groundwater by the velocity provides the time for moisture to travel from the surface or from the buried waste to groundwater.

In mathematical form, the governing equations are as follows:

$$V = r/\Theta \quad (1)$$

and

$$T = D/V \quad (2)$$

where:

V = velocity (cm/yr)
r = recharge rate (cm/yr)
Θ = volumetric water content (mL/cm^3)
T = travel time to groundwater (yr)
D = depth to groundwater (cm).

By rearranging equations 1 and 2, the recharge rate can be determined. Discussion and derivation of these equations are available in Heller *et al.* (1985) and Hillel (1980).

Lysimeter Description. In 1971, two large lysimeters were installed 1.6 km south of the 200 East Area (Figure 1). These lysimeters are approximately 3 m in diameter and 18 m deep.

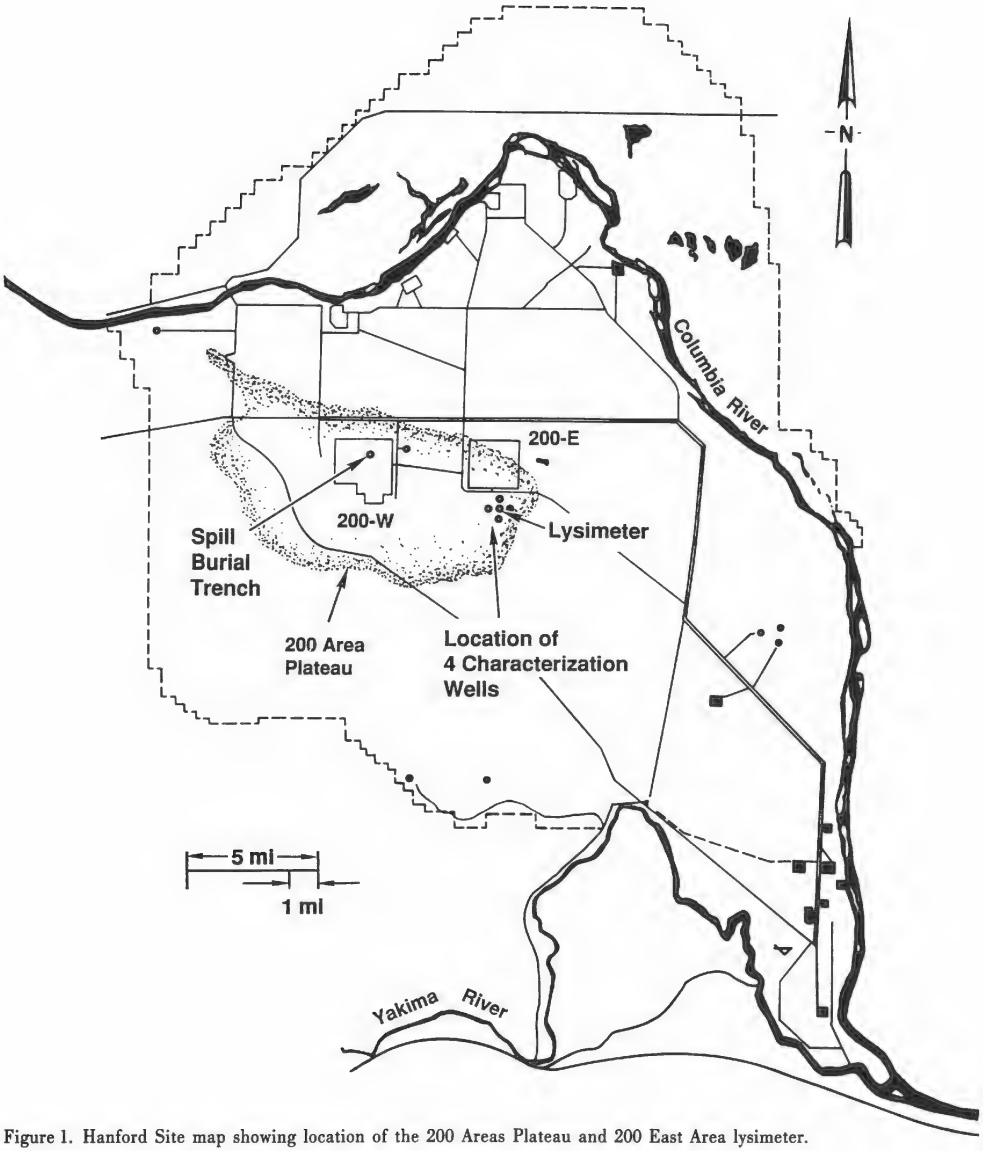
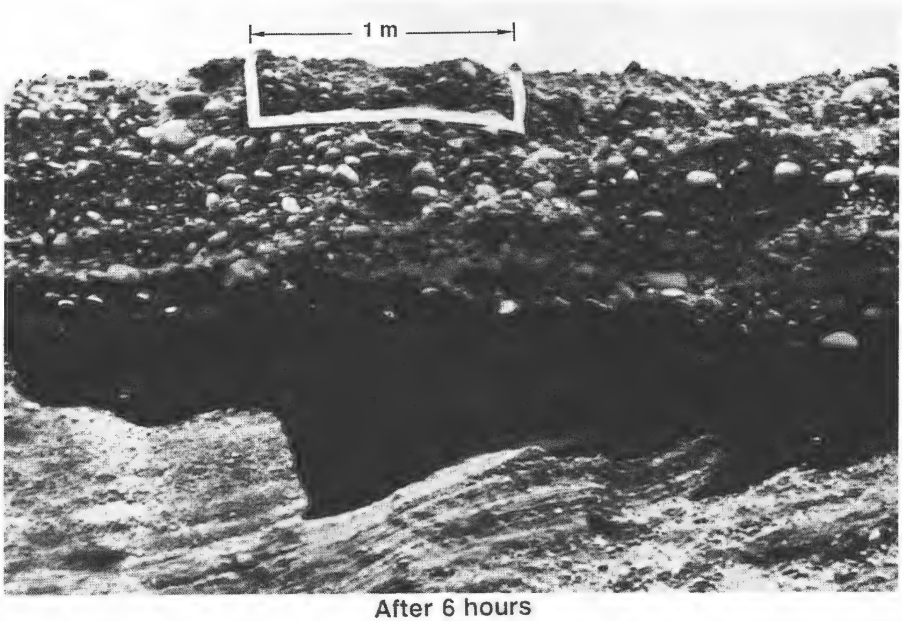
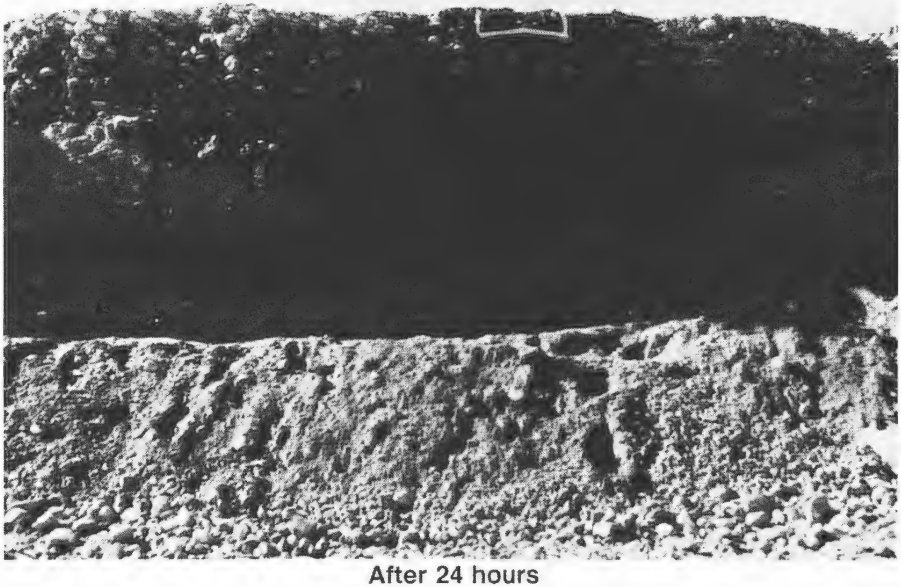


Figure 1. Hanford Site map showing location of the 200 Areas Plateau and 200 East Area lysimeter.

Both were equipped with instruments to evaluate possible vertical movement of soil moisture. One lysimeter was left open at the bottom, while the other was sealed at approximately 18 m (Figure 3). Any large amount of downward moisture movement was projected to result in an accumulation of recharge moisture in the lower portion of the closed-bottom lysimeter. Three 4.09-cm access tubes for neutron moisture probes were installed in each lysimeter to permit measurement of the moisture content at various depths. A lysimeter deters lateral moisture flow, making the lysimeter data amenable to one-dimensional analyses. These lysimeters are described in detail in



a)



b)

Figure 2. Typical horizontal and vertical movement of liquids in Hanford Formation sediments under partially saturated conditions: a) after 6 hr, and b) after 24 hr. Taped area outlines location (1 m in width) of water addition.

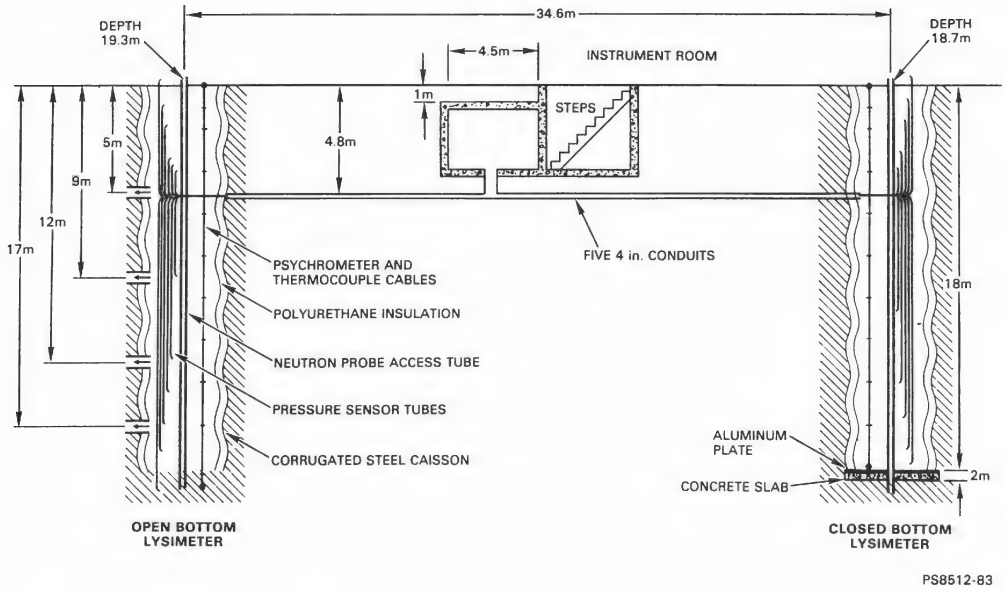


Figure 3. Cross-section view of the 200 East Area lysimeter.

Hsieh *et al.* (1973). The open-bottom lysimeter was subsequently dismantled and will not be considered in this analysis.

Neutron-moisture data were collected from the lysimeter for several years; however, neutron-moisture data are not sufficiently precise or accurate to measure the small changes in the lysimeter's moisture content which occurred (Jones 1978). Thus, the recharge was calculated from the initial and 1985 gravimetric moisture data (Hillel 1980). When the sediment was packed in the lysimeter, the initial moisture content of the sediments was gravimetrically measured (Hsieh *et al.* 1973). Unfortunately, Hsieh *et al.* (1973) did not measure the textural composition of the soil or sediment in the lysimeter; however, characterization data on four wells surrounding the site within 600 m of the lysimeter are available (Routson and Fecht 1980). Average percentages of sand, silt, and clay for the top 18 m of the four wells are 88.7 ± 0.57%, 9.4 ± 0.55%, and 2.0 ± 0.23% (standard deviation), respectively (n = 51). These average percentages are judged to be representative of the homogenized soil or sediment that was excavated from the lysimeter site and packed into the caissons (Figure 3). In addition, pH values, $CaCO_3$ percentages, moisture potentials, field moisture percentages, bulk densities, and cation exchange capacity values are available for the four wells (Routson and Fecht 1980).

During much of the lysimeter's 13-yr history, the surface of the lysimeter was maintained unvegetated with nonselective herbicides; however, some cheat-grass (*Bromus tectorum*) plants (a shallow-rooted, introduced, annual grass) were observed following termination of the herbicidal treatment (ca 1980).

After 13 yr, the moisture content of the lysimeter sediment (soil) was remeasured, and recharge was estimated from the difference between current moisture content and initial moisture content. Samples were obtained by core drilling and hand sampling the lysimeter sediment. Samples were taken at approximately 1.5-m depth increments and then quickly placed in moisture cans, and the lid-can contact wrapped with tape. Moisture content was determined by the gravimetric method of Gardner (1965).

Solid-Waste Burial Ground

In 1970, a radioactive spill into the surface soil occurred on the Hanford Site. The contaminated soil was buried beneath approximately 4.7 m of

backfill in the 200 West Area solid-waste burial ground (Figure 1) on a generally unvegetated site; however, sparse Russian thistle (*Salsola kali*) was observed in 1980 (see leveled area in immediate background of Figure 4; all identifiable vegetation is Russian thistle). In 1980, as part of a solid-waste burial-ground study, the surrounding soil was cored and sampled with a split spoon coring device (Figure 4) to determine how deep the waste might have leached (Routson *et al.* 1981b).

Results and Discussion

Lysimeter

There has been some redistribution of moisture from the upper half of the lysimeter to the lower half of the lysimeter (Figure 5) because surface sediments in 1971 were somewhat wetter than the deeper sediments. The upper 3 m show a seasonal variation (Hsieh *et al.* 1973, Brownell *et al.* 1975, Last *et al.* 1976, Jones 1978). The observed redistribution represents an approach to a steady-state system and *not* recharge.

It can also be seen in Figure 5 that for the period 1972 to 1985, the moisture content decreased in the zone from 3 to 9.9 m. In contrast, the moisture increased from 9.9 m to the bottom of the lysimeter. The moisture content is seasonally variable in the zone from the surface to 3 m and must be ignored in the calculation. The net moisture change is calculable from the difference in the areas between the areas of moisture gain and loss. In this case, the difference is so small that it is probably not significant; but, there is apparently a small net loss of moisture which translates to a negative recharge. Since the net change is so small, it is taken as zero within the error of measurement. Because there is no measurable (net) accumulation of moisture in the lysimeter, recharge is estimated at 0 ± 0.2 cm/yr (two sigma uncertainty). Thus, the apparent upper-bound of the recharge rate is taken as <0.2 cm/yr.

A greater amount of moisture would likely be removed (i.e., by evapotranspiration) on an undisturbed, lightly disturbed, or revegetated site (if there were any more moisture available). However, note that a significant potential for recharge may exist where vegetation and fine-textured soils have been removed and/or replaced with coarse-textured soils or gravel, as is the case at many of the waste sites on the 200 Areas Plateau. Experimental studies are under way at Hanford to determine optimum conditions for infiltration barriers in these cases (Adams and Wing 1986).

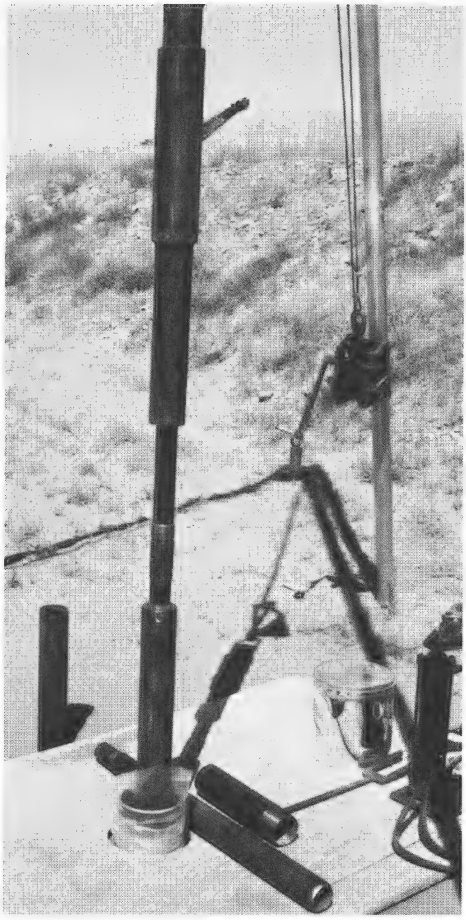


Figure 4. Split spoon coring device in use at the solid waste burial ground, 1985.

It should also be noted that evaporation from a bare soil surface has often been shown experimentally to exceed evapotranspiration from the same vegetated soil type. This likely occurs because the relative humidity near the soil surface is maintained at a much higher level, decreasing evapotranspiration losses. This effect is especially true for the light-textured (sandy) soil at the Hanford Site 200 Areas Plateau (Aase and

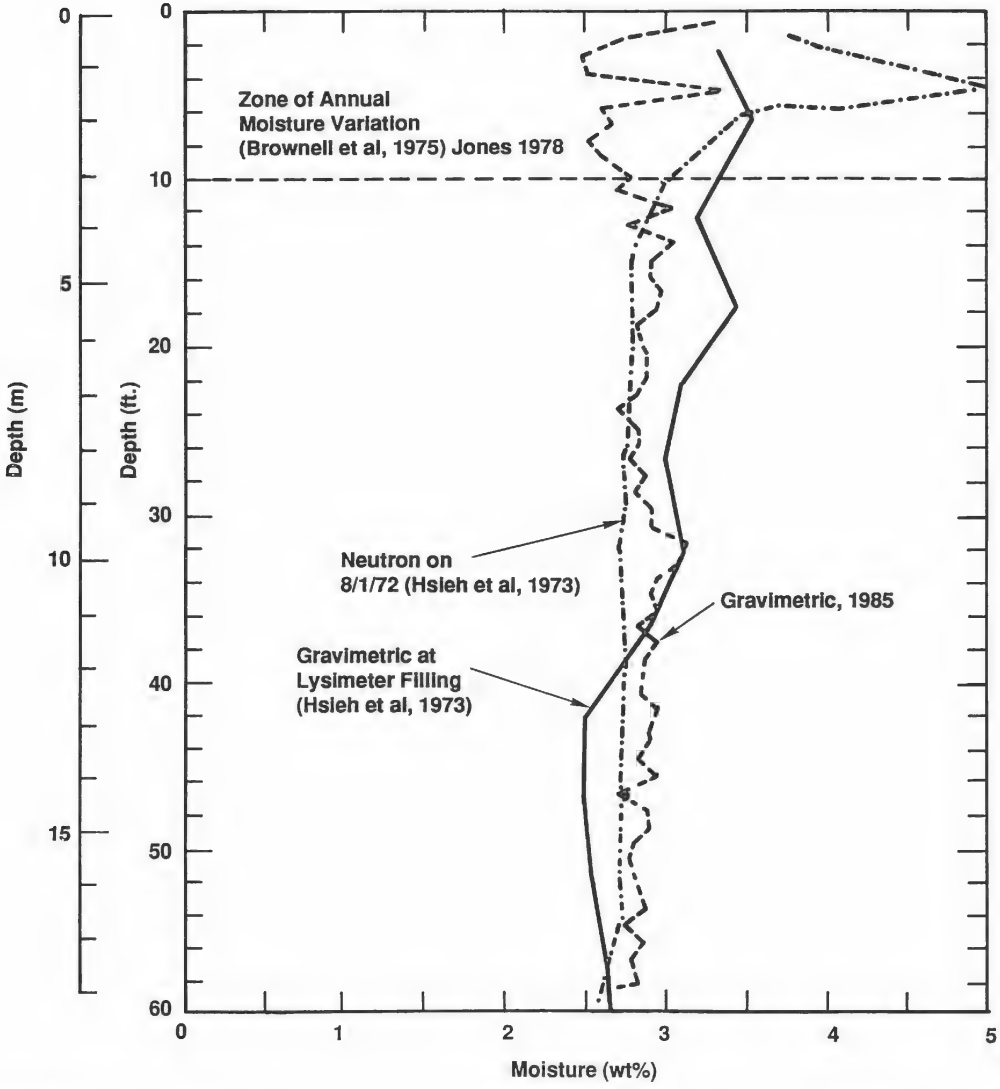


Figure 5. Gravimetric moisture content distribution for 1985 (dashed curve) and 1972 (solid line) in the 200 East Area closed-bottom lysimeter.

Siddoway 1982, Aase and Tanaka 1987, Black *et al.* 1969, Lascana and van Bavel 1983, Mapa *et al.* 1986, and Silkworth and Grigal 1982). In addition, high wind velocities often follow any rainfall at the Hanford Site, further increasing evaporation. Thus, a limited portion of the precipitation was probably removed by plant transpiration.

Burial Ground

Figure 6 is a representation of the measured ^{137}Cs activity as a function of depth. This figure demonstrates that there was no measurable activity below the bottom of the burial trench. However, there was increased ^{137}Cs activity above the top of the waste. This suggests that the net movement of moisture was upward during the

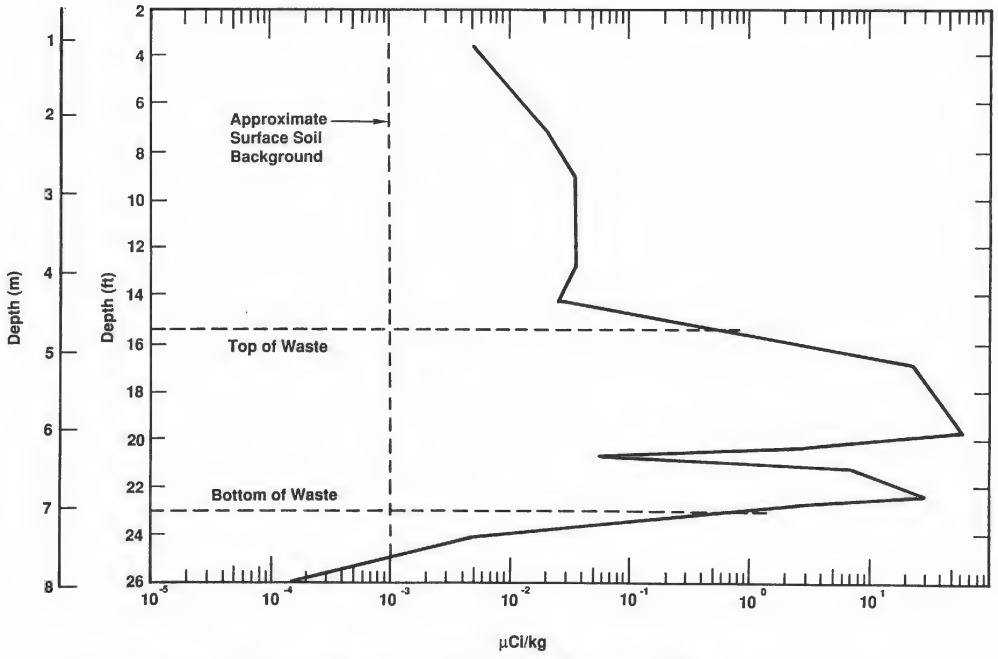


Figure 6. Cesium-137 depth profile through waste burial trench, 200 West Area, 1980.

storage period, and the net recharge is zero, and probably negative, over the 10-yr burial period.

The chemical matrix of the ^{137}Cs spill was a multimolar NH^{+}_{4} solution, which has been demonstrated to cause a large decrease in the sorption of cesium (Jacobs 1960; Routson *et al.* 1981a). In addition, water and soil were added to the spill during cleanup operations to prevent airborne dispersion during handling. Thus, a large moisture gradient existed between the buried waste and the essentially air-dried backfill material causing transport toward the soil surface. Also, Russian thistle is a deep-rooted plant which may have contributed to upward movement of ^{137}Cs (Routson and Cataldo 1978).

Conclusions

Recharge was 0 ± 0.2 cm/yr based on a 13-yr period of moisture accumulation in the Hanford Site 200 East Area closed-bottom lysimeter. Recharge based on field observations was further evaluated using radionuclide depth-distribution data from a decade-old burial trench. Waste transport in a solid-waste burial trench appeared to be upward, suggesting zero or negative recharge. Thus, the field record of waste movement over a 10-yr period was in good agreement with the lysimeter study, confirming that recharge was small and probably approached zero under the environmental conditions at these two sites during the period of observation.

The significance of these observations is that there appears to be very little potential for downward movement of mixed waste contaminants in the upper vadose zone under conditions that exist over much of the 200 Areas Plateau (i.e., areas of the plateau with natural or minimally disturbed soil profiles and vegetative cover and/or areas where the natural surface or near-surface conditions can be easily restored). Current waste management practices as well as closure plans for waste cleanup should strive to maintain or enhance this natural, beneficial feature of the 200 Areas Plateau at the Hanford Site.

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Avalanche-Generated Debris Flow of 9 May 1986, at Mount St. Helens, Washington

Abstract

On the evening of 9 May 1986, a hot, newly extruded portion of the lava dome in the crater of Mount St. Helens collapsed onto the late spring snowpack, generating a flow which traveled the length of the crater with an average velocity of 5 m/s. At Loowit gaging station, 2.4 km from the dome, the flow had an instantaneous peak discharge of 230 m^3/s and was a high discharge water event, not a debris flow. However, within the next 1-2 km the flow incorporated sufficient solids to evolve into a debris flow with a velocity of 5.5-6.5 m/s and a peak discharge of 870 m^3/s. The debris flow attenuated rapidly upon reaching the flat expanse of Step Fan and left recognizable deposits for only 3 km beyond the base of the mountain. Small-scale events such as this are probably quite common in the eruptive history of a volcano but are rarely preserved in the stratigraphic record. Recognition of such events as a component of eruptive activity is important in creating a realistic volcanic hazards assessment of individual volcanoes.

Introduction

On 9 May 1986, at 1948 PDT (Pacific Daylight Time), the upper two flood warning switches in a tier of four at Loowit gaging station (Figure 1) tripped, indicating a flow having a depth of at least 1.8 m (height of the uppermost switch above mean water level) had passed the station. Concurrent telemetered data from seismographs located near the mountain indicated a large, prolonged event was occurring within the crater. These events represented the culmination of two weeks of increasing seismicity and deformation of the dome within the crater of Mount St. Helens that had led to the prediction of an imminent eruptive event, probably a dome-building eruption. Because of this prediction, personnel at the Cascades Volcano Observatory were keeping a 24-hour watch over the telemetered data at the time the switches tripped. Seismographs located 5.5 km and 11.5 km from the crater recorded only background or low-level seismicity, not the gradually increasing, prolonged signal associated with lahars flowing along the upper North Fork Toutle (Brantley *et al.* 1985). Elk Rock gaging station, 23 km flow path west from the crater, showed no abrupt increase in stage that would be indicative of a large, potentially dangerous flow. The scientist on duty therefore decided that the event was not large enough to necessitate immediate mobilization of field study crews or to present a hazard to downstream property.

It was not until 12 May that the authors were able to make a short reconnaissance visit to the Loowit Ravine-Step Fan area. Through marginal weather, evidence of flooding in Steam and Lake Creeks and a veneer of boulder litter and granular debris on the central and eastern portions of Step Fan was readily apparent, as was a slump scar on the east wall of Loowit Ravine downstream from Loowit Falls. In the crater, a large avalanche deposit at the base of the talus chute on the north side of the dome was also observed. The avalanche occurred when a large piece of the hot, newly extruded lobe detached from the main mass on the top of the dome and tumbled down the steep northern face, fragmenting as it went. Evidence of flow was obvious from the toe of the avalanche deposit to the head of Loowit Ravine (Figure 2).

Deposits and Interpretations

The hot avalanche and accompanying surge of hot ash and gases (Mellors *et al.* 1988) induced rapid melting of the crater floor snow cover and created a flow which entered the main crater drainage system. Aerial reconnaissance of the head of Loowit Ravine showed that deposits from this flow veneered the late spring snow-pack, attesting to the generally passive, non-erosive nature of the early stages of the flow. These deposits were not investigated on the ground by the authors owing to time constraints and the unstable and therefore unsafe nature of the ravine walls upstream from Loowit gaging station.

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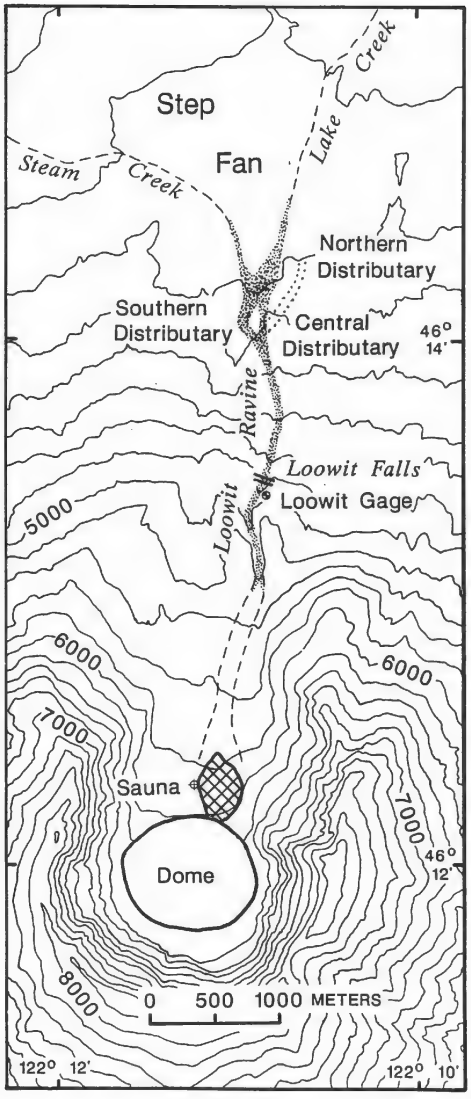

Figure 1. Location map showing pertinent sites. Portions of the flow studied are stippled, the avalanche from the dome is cross hatched. Base map is from U.S. Geological Survey preliminary maps, 1981 topography, 1:24,000. Contour interval is 200 feet.

At Loowit gaging station, the upper two flood-warning switches tripped at 1948 PDT; the two lower switches did not transmit and apparently were carried away or incapacitated before they could trip or were inoperable at the time of the event. The fact that both upper switches tripped at the same time indicates a very rapid rise in stage; essentially a wave at least 1.8 m high. A telemetered tiltmeter, located 300 m north of the base of the dome at a research site named Sauna, made its last routine transmission at 1940 PDT (it was programmed to transmit at 10 minute intervals) and did not transmit again. Crews visiting the crater on 14 May found that the tiltmeter had been destroyed by the avalanche, apparently sometime between its last transmission at 1940 PDT and its next scheduled transmission time of 1950 PDT. Assuming the event that destroyed the tiltmeter was the same event that initiated the flow (there may have been multiple episodes of avalanching over the space of a few minutes), travel time of the flow from Sauna site to Loowit gaging station was a maximum of 8 minutes. Estimating a flow path of 2.4 km from Sauna to the gaging station from existing maps yields a minimum average velocity of 5 m/s for the flow through the crater and the upper portions of Loowit Ravine.

Deposits near Loowit gaging station consist of 0.2 to 0.5 m of discontinuously bedded, fines depleted, coarse sand and gravel that form a terrace on the left bank along the outside of a gentle bend. A sandy coating covered rocks on the right bank below the high water mark. The incipient bedding and fine-grained nature of the terrace deposits indicate they were emplaced by a fluvial event, probably a clearwater or muddy flood, not a debris flow. Well-defined lower and horizontal upper surfaces of the terrace combined with a lack of well-developed bedding argues for a single event, not a succession of waves. An indirect estimate of flow made at the gaging station based on surveyed slope, cross-sectional area, and roughness of the channel, gives an instantaneous peak discharge at the gage site of about 230 m^3/s (T. Hale and D. Childers, oral communication, 1986).

Just downstream from Loowit gaging station, the channel drops abruptly over 75 m at Loowit Falls. At the base of the falls the flow apparently undercut the right bank of the ravine and initiated a partial bank collapse approximately 50 m long by 30 m high and of unknown thickness. Rubble from this collapse may have temporarily dammed the flow and eventually all of the loose material was incorporated into the flow. It was

Figure 2. View looking SSE into the Crater, showing avalanche deposit at the base of the dome and the flow markings leading to the head of Loowit Ravine (lower left corner). The newly erupted lobe is shrouded in steam at the top of the dome.

through incorporation of the bank collapse material and of channel bank and floor sediments in the reach directly downstream from the base of Loowit Falls that the flow bulked up sufficient solids to evolve into a debris flow. The debris flow apparently dammed and remobilized a number of times in the narrow, twisting, bedrock channel below Loowit Falls, creating a series of terraces 3 to 4 m high. These terraces possess essentially horizontal upper surfaces and formed when the debris flow momentarily slowed during the damming episodes. Because they do not parallel the local stream gradient, the terraces thin rapidly and disappear upstream. Material composing the terraces consists of unsorted, angular clasts up to 2 m across set in a sand-gravel matrix. The deposit is massive and generally ungraded, though a slight concentration of large clasts in the lower central portion of the deposit was occasionally apparent.

A large part of the material incorporated into the debris flow came from channel floor debris and the apron of talus along the walls of the ravine. This is supported by the observation that about 50 percent of the gravel- and sand-size matrix clasts were composed of dome-derived phaneritic dacitic debris carried from the avalanche by the initial stages of the flow, but essentially all of the cobble-size and larger clasts were from dark, aphanitic basaltic and andesitic flows which form the lower slopes of the mountain beyond the crater. The ravine downstream from Loowit gaging station is floored over its entire length by resistant lava flows, but much of the ravine wall is composed of fragmented pyroclastic debris or the shattered, ice-contact basal zones of stratigraphically higher lava flows. The walls usually possess an extensive talus apron of coarse material and the channel floor is littered with bouldery debris. However, when the ravine was visited one week after the flow, none of this easily erodible material was present. The channel floor was almost devoid of loose material and the walls were vertical with no talus development.

Loowit Ravine divides into 3 distributary channels, known as the north, central and south

distributaries, about 200 m upstream from Step Fan (Figure 1). Two of these distributaries, the northern and the southern, are occupied only during extreme discharge events; the central distributary is the channel which contains normal stream flow. A portion of the debris flow broke out of the central distributary through a depression in the ravine wall on the outside of a gentle, right-hand bend and entered the southern distributary channel; none of the debris flow entered the northern distributary. This breakout occurred when the debris flow ran along a bedrock shelf and then super-elevated over a vertical wall resulting in a total height gain of at least 8 m. The cross-sectional area of the flow through the depression (estimated from strand lines seen on scaled oblique photos) is about 50 m^2. Based on this area and the average velocities derived at the mouth of the central distributary (as discussed below), an instantaneous peak discharge of 300 m^3/s is estimated for the portion of the flow passing through the depression.

The deposit formed at the mouth of the southern distributary where it emerges onto the gently sloping, low relief surface of Step Fan, possesses a well defined left lateral boulder levee and contains clasts up to 2 m in diameter, but is generally less than 10 cm thick. The course of a small, intermittent stream which passed in front of the mouth of the southern distributary was covered for a distance of over 100 m by the deposit. However, the stream still appears to be following its pre-event channel and was not permanently dislocated by the debris flow. This observation suggests that, while the instantaneous peak discharge was very high, the actual volume of material in the flow was small and the resulting deposit was merely a veneer of insufficient thickness to permanently change the course of the stream.

Along the last 50 to 100 m of the central distributary, boulder levees found along the right bank of the gully delineate the peak height of the flow at 4 m above the channel bottom. The area between the levees is covered by only a scattering of clasts larger than gravel size and in places exhibits longitudinal scour marks. These scour marks and the lack of deposits indicate that the debris flow was still actively eroding and bulking-up as far as the mouth of the central distributary. Beyond the mouth of the central distributary is a deposit consisting chiefly of large, angular boulders of red and black flow rock, generally between 0.5 m and 2 m in diameter but ranging to over 3 m, eroded from the slopes of the mountain. A massive, 4- to 6-cm-thick, medium to coarse sand and gravel layer from the matrix of the debris flow covered the ground between the large clasts beyond the mouth of the distributary and veneered snow drifts immediately behind but lower than the tops of the levees mentioned previously. A hand lens inspection revealed that about 50 percent of this sandy deposit consisted of granular dacite and phenocrysts from fragmented dome rocks, the remainder being fine-grained, dark rock fragments incorporated from the channel below Loowit Falls.

For about 50 to 100 m downstream from the mouth of the central distributary at Step Fan, a coating of the sandy matrix material could be found on all boulders, even those near the center of the flow path, suggesting that a single, large surge or wave occurred and was not followed by a sustained recessional flow. This coating was fairly non-cohesive and had slid off boulder surfaces steeper than 30° to 40°. A broad, shallow channel about 0.3 to 0.5 m deep and tens of meters wide was incised into the fan near the right margin of the flow in this area. The cut face from this incision was also coated with the sandy, matrix material, indicating that the incision occurred early in the event, not by recessional flow. Margins of the deposit were sharp and well-defined, tapering to a thickness of 1-2 cm. By 12 May the deposit had de-watered and was not thixotropic.

Beyond 50 to 100 m from the mouth of the central distributary the deposits no longer resembled those of a debris flow but instead were the incipiently bedded sand and gravel material of a flood deposit. The debris flow must have started de-bulking immediately upon leaving the confines of the gully, depositing all of its cobble- and boulder-sized clasts and most of its matrix material within 100 m of the mouth of the distributaries.

At the mouth of the central distributary, the flow left noticeable mudlines that displayed run-up of 1.5 to 2 m on vertical walls and splashes from turbulence to over 3 m (Figure 3). Velocities inferred from the run-up range from 5.5-6.5 m/s (based on the formula $V = (0.5gh)^{0.5}$, where "V" is the velocity, "g" the gravitational constant and

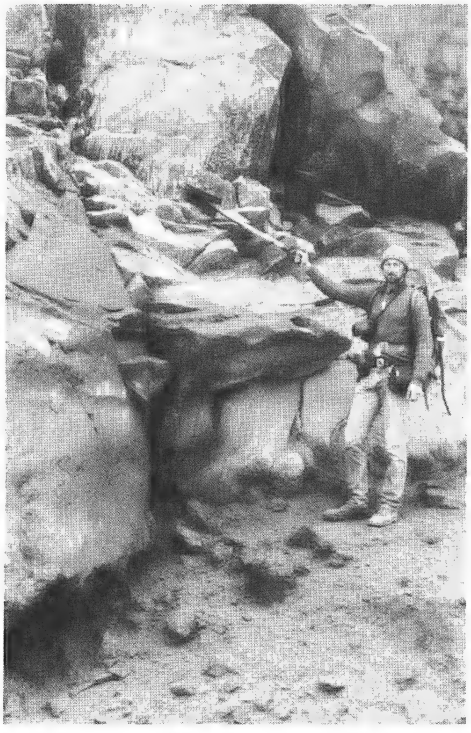

Figure 3. Run-up of about 2 m (mudline is near tip of shovel) on a vertical wall near the mouth of the central distributary. Note splash marks up to 3 m above ground level and lack of clastic debris on the channel floor.

"h" the height of the run-up). A "tape and Brunton" survey of the channel gave a cross-sectional area of 95 m^2, which, when combined with the average velocity, yields an estimate of 570 m^3/s for the instantaneous peak discharge at the mouth of the central distributary. Combined with the flow estimate from the southern distributary (300 m^3/s), the total instantaneous peak discharge for the event was about 870 m^3/s. Even though this value may seem extreme (the flood of record, 1981 to 1986, for Tower gaging station on the main stem of the Toutle River is 1,076 m^3/s; McGavock *et al.* 1986), it must be remembered that this flow, while possessing a very large instantaneous peak discharge, probably lasted for only a matter of seconds and was not a sustained event.

The rapidly attenuating flow from the southern and central distributary channels united along the west side of Step Fan before entering the system of gullies that drain the fan. About 70 percent of the flow entered Lake Creek and eventually reached Spirit Lake at its southwest shore. About halfway between Step Fan and Spirit Lake (1.5 km from the mouth of the central distributary), velocities calculated from run-up on large boulders were 1-2 m/s. Deposits in this area consisted of less than 0.3 m of discontinuously bedded fluvial sand and gravel. The remaining 30 percent of the flow went into Steam Creek. Deposits along this channel, while not visited on the ground, appeared from the air to form a veneer on low (1 to 2 m above water level) stream terraces as far downstream as 3 km from the Step Fan.

Summary and Discussion

The failure of a portion of a hot, newly extruded lobe on the dome at Mount St. Helens onto the late spring snowpack generated a flow which moved out of the crater through Loowit Ravine. Based on examination of deposits at Loowit gaging station, the flow above Loowit Falls was not a debris flow. By timing the interruption of telemetered data from instrumentation near the dome and the tripping of flood warning switches at the gaging station, a minimum average velocity of 5 m/s was calculated for the flow through the crater. An indirect estimate of flow at the gage site yielded a peak instantaneous discharge of 230 m^3/s.

Below Loowit Falls, deposits indicate that the flow had bulked up to a debris flow. This was accomplished through incorporation of coarse talus and channel floor sediments and through entrainment of material from a slump immediately below the falls. The presence of numerous tapering terraces suggest that the debris flow moved by damming and breaching.

Near the base of the mountain, a portion of the flow broke out of the main channel and emerged onto Step Fan through the southern distributary. An estimated instantaneous peak discharge of 300 m^3/s escaped into this channel.

The bulk of the flow reached Step Fan through the central distributary. Velocities calculated from run-up ranged from 5.5 to 6.5 m/s. An instantaneous peak discharge for this channel was estimated at 570 m^3/s. Flow from the two distributaries attenuated rapidly upon reaching Step Fan and merged into a single flow. This flow then divided once again with about 70 percent of the remaining volume entering Lake Creek. Less

than 2 km downstream on Lake Creek the flow had decreased to a depth of less than 0.3 m and a velocity of only 1 to 2 m/s. The remaining 30 percent of the flow left recognizable deposits for at least 3 km along Steam Creek, mainly as thin sediment veneers on low-lying stream terraces.

The combined instantaneous peak discharges from both distributaries was about 870 m^3/s, yet deposits were recognizable for only about 3 km beyond the mouth of the distributaries. Apparently this very high discharge occurred in the form of a single wave or surge that lasted only a matter of seconds. Therefore, even though the instantaneous peak discharge was comparable to a major flood on the main fork of the Toutle River, the actual volume of material involved was small. Judging from splash marks seen on the channel walls (Figure 3), the flow was very turbulent, which suggests that at least a portion of its volume may have been entrained air. The dramatic increase in peak discharge from Loowit gaging station (230 m^3/s) to the mouth of the distributaries (870 m^3/s) resulted from the active incorporation of large amounts of loose debris from within the channels right up to the passage of the flow onto the lower gradient of Step Fan. Bulking-up by debris flows on the steep, upper slopes of volcanoes and the rapid switch to deposition with lessening gradient has also been documented on Mount Hood, Oregon (Cameron and Pringle, 1986). The average stream discharge in Loowit Ravine at Loowit gaging station is insignificant (less than 0.1 m^3/s, T. Hale, oral communication, 1986). This would mean that the majority of the increase in discharge was in the form of coarse material possessing little interstitial fluid, with relatively minor amounts of water incorporated from stream flow within the channel. This probably explains the rapid attenuation of the flow upon reaching Step Fan; there was insufficient water to keep the solid portion of the flow mobilized except in confined, high gradient reaches.

Events such as this underscore the problems encountered in volcanic hazards assessment. Though small in scale, this flow moved at high velocities through an area soon to be opened to the public. Given the velocities calculated and the length of the flow path, the initial wave of the event may have reached the Step Fan area in as little as 10 to 12 minutes and with almost no warning.

A year after this event no identifiable deposits could be found to document this debris flow. The limited distribution of the deposits and the rapidly changing topography of the area had erased all evidence of this event. Assessment of hazards at most volcanoes is accomplished through examination of past eruptive events preserved in the stratigraphic record. Many events, such as the 9 May, 1986, debris flow at Mount St. Helens may simply not be preserved and bias the picture of a volcano's activity toward the larger phenomenon.

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Received 27 November 1989
Accepted for publication 19 January 1990

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Lithofacies and Sedimentology of the Miocene-Pliocene Ringold Formation, Hanford Site, South-Central Washington

Abstract

The Miocene-Pliocene Ringold Formation is one of the principal stratigraphic units within the suprabasalt "unconfined" aquifer at the Hanford Site in southcentral Washington. Consequently, understanding the geology of the Ringold Formation is necessary for the accurate characterization and modeling of groundwater flow and contaminant transport at Hanford. The Ringold Formation is a complexly interstratified sequence of unconsolidated to semiconsolidated clay, silt, sand, and granule to cobble gravel. Evaluation of borehole geological and geophysical data and outcrops on and adjacent to the Hanford Site suggests that the most accurate method for the study of Ringold sediments is through the use of lithofacies. Six lithofacies are defined using primarily grain size data and borehole geophysical responses. These lithofacies are: 1) mud (M), 2) mud and sand (MS), 3) sand (SS), 4) sand and granule to pebble gravel (SG), 5) granule to pebble gravel (G), and 6) cobble to boulder gravel (CB). Analysis of lithofacies distributions and associations reveal that: 1) coarse-grained lithofacies (CB, G, SG, SS) tend to be concentrated along complexly stacked, elongate fluvial channel tracts that display a high degree of vertical interconnectedness, 2) fine-grained lithofacies (M, MS) tend to occupy relatively stable positions, and 3) individual lithofacies identified at the Hanford Site tend to be discontinuous even over short lateral distances. Based on the analysis of lithofacies distributions and associations more accurate appraisals of the hydrogeology of the Hanford Site are possible.

Introduction

Thousands of tons of radioactive and other hazardous wastes have been introduced into the late Cenozoic sediments on the Hanford Site, Washington, since the late 1940's (PNL, 1986, 1987). The accumulation of these wastes has necessitated a long-term program of groundwater monitoring and geohydrologic characterization of the unconfined aquifer to assess the extent of present and potential future groundwater contamination in this area. The Miocene-Pliocene Ringold Formation is the principal stratigraphic unit within the suprabasalt "unconfined" aquifer; thus, its stratigraphic and sedimentary complexities are important to the characterization of the groundwater flow system. A fundamental parameter in stratigraphic and sedimentary studies are lithofacies (Miall 1977, 1978; Rust 1978).

This paper presents findings from a study of primarily subsurface lithofacies identified in the Ringold Formation on and immediately adjacent to the Hanford Site. The paper reevaluates the five-tiered subdivisions of the Ringold Formation generally used at the Hanford Site (Myers *et al.* 1979; DOE 1988), suggests alternative methods for characterizing these strata, and presents sedimentological interpretations.

Geologic Setting

Suprabasalt terrigenous clastic sediments (Figure 1), including the Ringold Formation, are present throughout much of the central Columbia Plateau in south-central Washington (Grollier and Bingham 1971, 1978; Myers *et al.* 1979; Tallman *et al.* 1979, 1981; Fecht *et al.* 1985). Regionally, the Ringold Formation consists of up to 280 m of interstratified unconsolidated to cemented clay, silt, sand, and granule to cobble-sized gravel deposited in fluvial and lacustrine settings (Newcomb 1958; Bjornstad 1985; Fecht *et al.* 1985; DOE 1988). Exposures of the Ringold Formation are limited because of an extensive Pleistocene-Holocene sedimentary cover and erosion by catastrophic, proglacial Pleistocene floods. However, informative outcrops exist; 1) on the White Bluffs north and east of the Columbia River, 2) in ravines and coulees between Wallula Gap and Moses Lake, Washington, and 3) near prominent anticlinal ridges including Rattlesnake Mountain, the Saddle Mountains, Gable Mountain, and the Frenchman Hills (Figures 2 and 3).

The Ringold Formation at the Hanford Site consists dominantly of sand and granule to cobble-sized gravel with lesser, yet still significant amounts of clay, silt, and sand (Newcomb

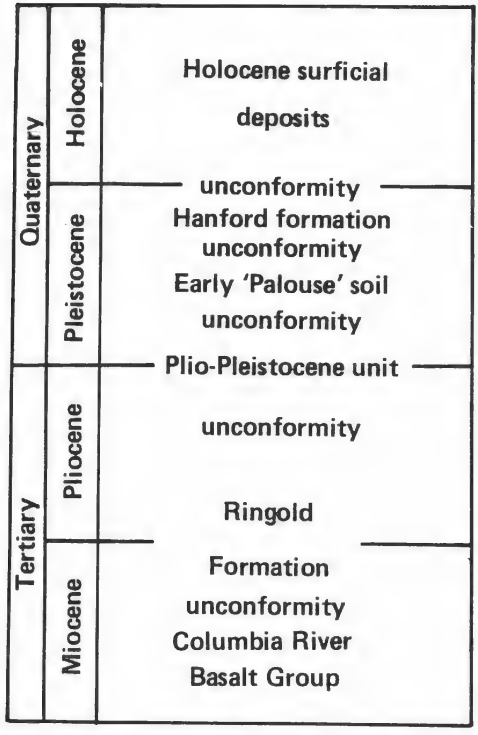

Figure 1. Generalized stratigraphy of the late Cenozoic sediments in the Pasco Basin, southcentral Washington.

1958; Newcomb *et al.* 1972; Myers *et al.* 1979; Tallman *et al.* 1979, 1981; Bjornstad 1984, 1985); it is greater than 50 m thick at most localities and reaches a maximum thickness of 260 m near the center of the Hanford Site. Exposures of the Ringold Formation along the White Bluffs (Figure 3) consist of up to 125 m of interbedded clay, silt, sand, and relatively minor granule to cobble gravel. These exposures generally lie stratigraphically above those Ringold strata described from the Hanford Site.

Ringold Formation strata originally were considered to be Pleistocene-aged (Merriam and Buwalda 1917, Newcomb 1958, Grollier and Bingham 1971, Newcomb *et al.* 1972). However, subsequent paleontologic, paleomagnetic, and palynologic studies have demonstrated a greater age for the Ringold. Gustafson (1973, 1980) and Packer and Johnson (1979) suggested a Miocene to Pliocene age based on paleomagnetic and paleontologic data from Ringold exposures and drill core, while Leopold and Nickman (1981) determined a Miocene age for the oldest Ringold strata on the basis of pollen samples collected near the base of the Ringold Formation. Fecht *et al.* (1985) established a maximum age of 8.5 Ma for the Ringold Formation from K-Ar whole-rock dating of the underlying Miocene basalt (McKee *et al.* 1977) and a minimum age of 3.4 Ma on the basis of paleomagnetic data and vertebrate fossil evidence.

Previous Studies

All suprabasalt sediments (including strata now assigned to the Ringold Formation) on the central Columbia Plateau and in the eastern foothills of the southern Washington Cascades were originally assigned to the Ellensburg Formation by Smith (1901). Smith's stratigraphy was later modified by Merriam and Buwalda (1917), who assigned the fine-grained terrigenous clastic sediments exposed on the White Bluffs and near Pasco, Washington to a unit they called the Ringold Formation. Culver (1937) later mapped the Ringold Formation across the central Columbia Plateau. Both Merriam and Buwalda (1917) and Culver (1937) restricted their definition of the Ringold Formation to strata exposed at the surface.

The concurrent establishment of the Hanford Site and expansion of nearby irrigated farmland in the early 1940's resulted in numerous test boreholes and production wells that revealed a sequence of buried sediments overlying the Columbia River Basalt Group. A significant proportion of these strata were found to be subsurface extensions of Ringold exposures found on the White Bluffs (Newcomb 1958). As a result, the Ringold Formation was redefined to include all sedimentary strata in the Pasco Basin that overlie the Columbia River Basalt Group and that underlie Pleistocene glaciofluvial deposits (Newcomb 1958).

The Ringold Formation as defined at the Hanford Site by Newcomb (1958) and Myers *et al.* (1979) is divided into the following five lithostratigraphic units. These are the: 1) gravel-dominated basal unit, 2) interstratified to mixed clay, silt, sand, and local gravel of the lower unit (including the prominent 'blue clays' of geologic drill logs), 3) quartzose gravel of the middle unit, 4) interstratified to mixed clay, silt, and sand of

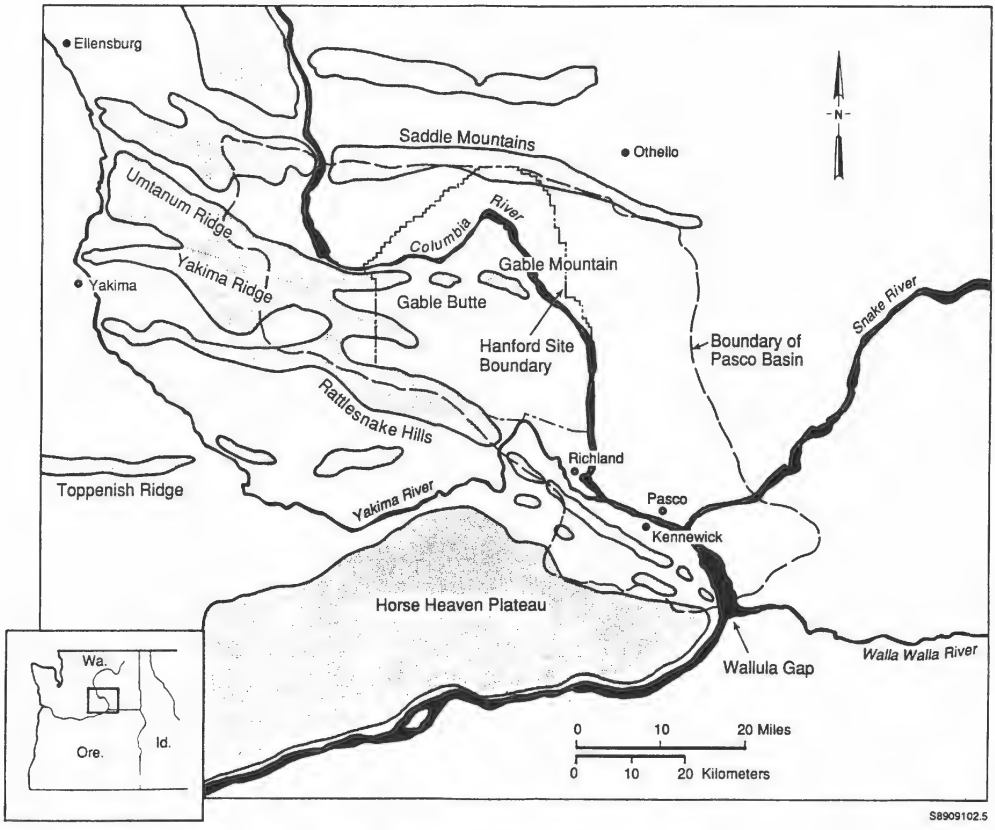

Figure 2. Geographic setting of south-central Washington and location of the Hanford Site.

the upper unit, and 5) locally-derived basaltic gravel of the fanglomerate unit. Only the fanglomerate unit, upper unit, and upper part of the middle unit crop out. Offsite the Ringold Formation has been subdivided on the basis of lithofacies (Grollier and Bingham 1971, 1978). These lithofacies are not the same as those defined in this report.

Methods

Discussion of the Ringold Formation in this paper is largely restricted to subsurface investigations at the Hanford Site (Figures 2 and 3); outcrops on the Hanford Site are uncommon and only occur along the flanks of a few anticlinal ridges. Borehole geologic logs, sediment samples, and accompanying geophysical data (primarily natural gamma and neutron-neutron logs) from 147 boreholes that extend to basalt were chosen for study. The majority of the sediment samples available from those holes are drill cuttings. Interpretative stratigraphic sections, that are constructed from this joint geologic/geophysical database, form the basis for identification and description of lithofacies and the construction of isolith, isopach, and lithofacies maps. Six lithofacies are defined primarily on the basis of grain size descriptions from geologic drill logs, textural analyses, and to a very limited extent, from borehole geophysical logs, cores, and outcrops. These lithofacies are: 1) mud (M), 2) mud and sand (MS), 3) sand (SS), 4) sand and granule to pebble gravel (SG), 5) granule to pebble gravel

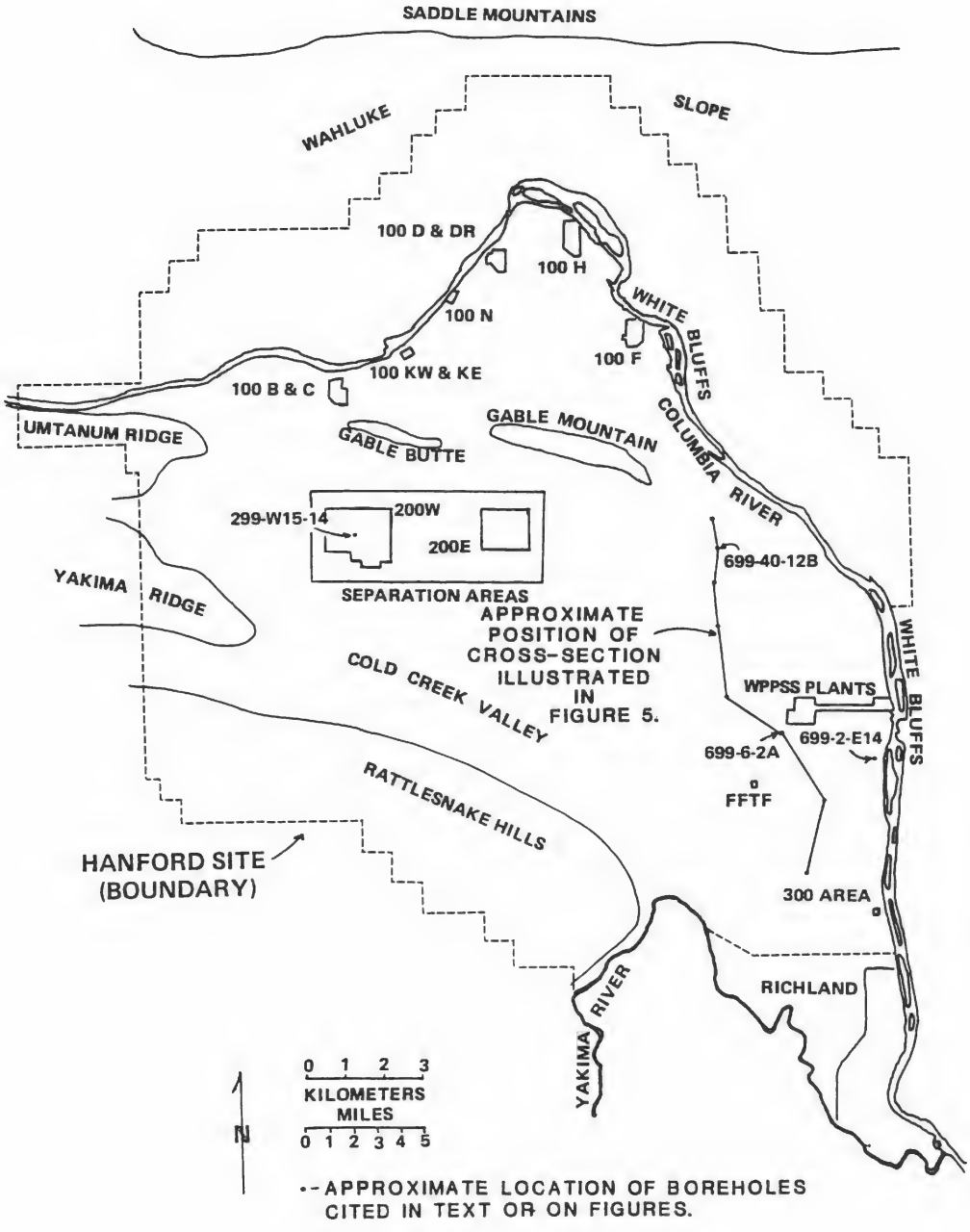

Figure 3. Location map of the Hanford Site modified from Tallman *et al.* (1979).

(G), and 6) cobble to boulder gravel (CB). The lithofacies code is loosely based on the set of codes introduced by Miall (1977, 1978) and Rust (1978) for studies in fluvial sedimentology. However, unlike the lithofacies identified by Miall and Rust, Ringold lithofacies are not further subdivided on the basis of primary sedimentary structures. This reflects the small number of intact cores available for study and the lack of clear correlation between drill cuttings and either cored samples or outcrops. This reliance on less than optimum subsurface data as well as the distances between boreholes (usually many hundreds to thousands of feet), limits but does not prohibit identification of the major depositional trends and large-scale architectural elements necessary to reconstruct depositional setting (Miall 1985, 1987).

Lithofacies Description and Interpretation

Lithofacies M: Mud

Lithofacies M (Figure 4) consists of massive to laminated gray, brown, olive, and blue clay and silt. Beds are a few centimeters to tens of meters thick and average less than 10 m thick. Sand comprises up to 10 percent of this lithofacies and occurs as thin (< 30 cm thick) lenticular interbeds and as intermixed grains. Meters-thick paleosols are common in core and surface exposures. Thin (< 10 cm), laterally extensive ash beds are present, but uncommon. Mud lithofacies tend to be discontinuous in the subsurface (Figure 5) and commonly grade down into muddy-sand (MS) and sandy-gravel (SG) lithofacies; they are most commonly overlain by gravel (G) and cobble-boulder (CB) lithofacies.

The fine grain size and generally good sorting indicate that this facies resulted primarily from suspension deposition in standing or slow-moving waters, probably in an overbank and possibly in a backwater swamp or lacustrine setting such as described for similar lithofacies by Miall (1977, 1978). Abundant paleosols indicate periodic subaerial exposure. The laminated clay and silt of this lithofacies have been interpreted as lacustrine (Bjornstad 1985). Thin sand beds are consistent with intermittent tractional transport of ripples and sheet sands (Miall 1977, 1978), probably during flood stage.

Figure 4. Thick laminated to thin bedded mud analogous to the type assigned to facies M. Gradations on Jacob staff are 10 cm.

Lithofacies MS: Mud and Sand

Lithofacies MS (Figure 6) consists of massive to interlaminated gray, brown, olive, and rarely blue clay and/or silt, and sand. Bedding thicknesses range from a few centimeters to less than 10 m. Sand contents range from 10 to 80 percent and average 50 percent. Climbing rippled and normally graded fine-grained sands in sets 20 to 40 cm thick and soft-sediment deformation is common in the lithofacies along the White Bluffs. Meters-thick paleosols are common in core and surface exposures while thin (< 10 cm) ash beds are less common. However, as in lithofacies M, paleosols and ashes are difficult to identify in borehole cuttings. Deposits of lithofacies MS

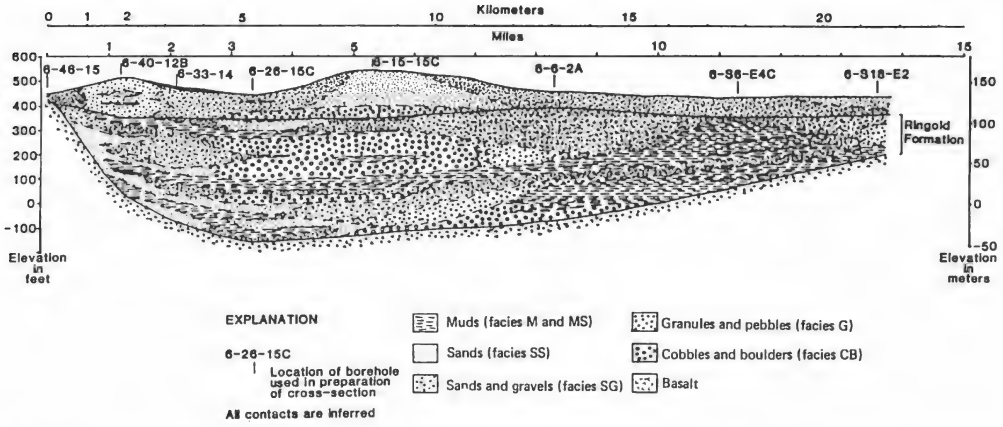

Figure 5. Geologic cross-section showing the marked lateral lithostratigraphic variability of the Ringold Formation. See Figure 3 for location of cross-section.

Figure 6. Strata typical of those assigned to facies MS. Dashed line separates sand (above) from mud (below). Note rock hammer for scale.

tend to be discontinuous, generally grade down into sand (S) and sandy-gravel (SG) lithofacies, are gradationally overlain by lithofacies M, and frequently are truncated and overlain by deposits of the gravel (G) and cobble and boulder (CB) lithofacies.

The mixed textural character of lithofacies MS implies that it resulted from episodic input of coarse-grained detritus transported into standing or slow moving waters by intermittent traction and possibly flood currents in an overbank to lacustrine setting. Miall (1977, 1978) and Galloway (1981) ascribe an overbank setting to similar fluvially-derived strata. The relatively high concentration of sand in this lithofacies as compared to that in lithofacies M suggests a more proximal location to stream channeling. Pedogenesis is consistent with a floodplain interpretation (Miall 1977, 1978). However, the presence of soft-sediment deformation indicates periodic rapid accumulation of sediment in deltaic and lacustrine settings.

Lithofacies SS: Sand

Lithofacies SS (Figure 7) consists of sand that is gray, olive, and less commonly, tan and brown, fine to coarse-grained, moderately to poorly sorted, subangular to subrounded, and unconsolidated to weakly cemented. Up to 20 percent of this lithofacies may be composed of mud, granules, and pebbles, most commonly as lenticular interbeds. Sand lithofacies in core and outcrop display massive bedding, plane to horizontal stratification, and planar and trough cross-stratification in 5 cm to 1 m thick tabular sets. Total thicknesses of lithofacies SS are generally < 10 m. Deposits of the sand lithofacies commonly grade upwards into lithofacies M, MS, and SG, and grade downwards into lithofacies SG, G, and CB. Lithofacies SS also sharply truncates lithofacies M and MS and is, in turn, truncated by lithofacies SG, G, and CB. Sand detritus is composed dominantly of quartz, feldspar, and mica grains, and with lesser granitic, basaltic, and gneissic lithic fragments.

Figure 7. Cross-bedded sand analogous to the strata comprising facies SS.

The coarse-grain sizes, and primary sedimentary structures are consistent with migration and aggradation of ripples, sand-waves, and plane beds (Miall 1977, 1978). The discontinuous nature of sand lithofacies suggest a channel-like character for these deposits. Deposition of lithofacies SS is inferred to have been confined to trunk and tributary channels, probably during normal stream flow and during the waning stages of floods when these sediments were deposited atop coarser-grained, gravel-dominated lithofacies.

Lithofacies SG: Sand and Gravel

Lithofacies SG (Figure 8) consists dominantly of gravel that is light to dark gray, poorly sorted, unconsolidated to poorly cemented, matrix- and clast-supported and granule- to pebble-sized. Sand and mud make up less than 50 percent of lithofacies SG and occurs as matrix and in lenses and beds up to 1 m thick. Limited outcrops of apparently analogous SG strata (Figure 8) occur in 1 to 20 m thick beds that exhibit large-scale trough and planar cross-strata, clast imbrication, meters-wide channel scours, and bar-shaped lenticular bodies. Deposits of the sand and gravel lithofacies commonly are gradationally overlain by lithofacies M and MS, are sharply to gradationally overlain by lithofacies SS, and gradationally overlie and are sharply truncated by lithofacies G and CB. Gravels are composed dominantly of quartzitic, basaltic, granitic, gneissic, and porphyritic volcanic clasts; sands generally are quartzo-feldspathic.

Deposits of the SG lithofacies are interpreted as mixed in-channel sediments. Deposition of cross-stratified, stratified, and imbricated gravel-dominated and sand-dominated lenses and beds reflect aggradation of transverse and longitudinal gravel bars and dunes (Miall 1977, 1978). The interstratification of sand and gravel, as well as the incorporation of sand as matrix and lenses is common to braid plain systems that experience widely fluctuating currents (Rust and Koster, 1984). Periodically strong stream currents are

Figure 8. Interbedded crudely stratified granule to pebble gravel and cross-stratified sand analogous to the strata comprising facies SG. Note rock hammer for scale.

implied by concentrations of pebble-sized gravel within this lithofacies.

Lithofacies G: Granule to Pebble Gravel.

Lithofacies G (Figure 9) consists dominantly of clast- and matrix-supported granule and pebble gravel that is light to dark gray, poorly sorted and unconsolidated to poorly cemented. Sand, mud, and cobble-sized gravel comprise less than 20 percent of the lithofacies. Sand and mud occur as both intermixed matrix and as <50 cm thick lenses; cobbles are present as floating grains. Limited outcrops of analogous strata (Figure 9) display 1 to 10 m thick intervals that exhibit large-scale trough and planar cross-strata, clast imbrication, meters-wide channel scours, and bar-shaped lenticular bodies. Upper and lower bounding surfaces of lithofacies G are sharp to gradational. Gravels are composed of quartzitic, basaltic, granitic, gneissic, and porphyritic volcanic clasts; sands generally are quartzo-feldspathic.

Deposits of lithofacies G are interpreted as in-channel sediments. Deposition of cross-stratified, stratified, and imbricated gravel-dominated beds reflect aggradation of transverse and longitudinal gravel bars and in-channel dunes (Miall 1977, 1978; Rust 1978). The interstratification of sand and gravel as well as the incorporation of sand and mud as matrix material and lenses is common to braid plain systems that experience widely fluctuating currents (Rust and Koster 1984). However, the concentration of granules and pebbles in this lithofacies attest to either consistently stronger currents, or a more limited and gravel-dominated source than is inferred for the SG lithofacies.

Lithofacies CB: Cobble and Boulder

Lithofacies CB (Figure 9) consists of lenses and beds of cobbles and boulders that are light to dark gray, massive to crudely stratified, matrix to clast-supported, poorly sorted, and unconsolidated to poorly cemented. The cobble and

Figure 9. Crudely stratified granule to pebble gravel of the type typical of strata comprising facies G interstratified with cobble and boulder gravel typical of facies CB. Gradations on Jacob staff are 10 cm.

boulder content exceeds 20 percent. Sand, mud, and granule to pebble-sized gravel can comprise up to 80 percent of the lithofacies and may occur as both matrix and as less than 1 m thick interstratified lenses and beds. Strata assigned to lithofacies CB form sequences 0.5 to 5 m thick. Lithofacies CB overlies sharply truncated surfaces and is overlain gradationally by lithofacies SG and G and rarely by lithofacies M and MS.

Deposits of lithofacies CB are interpreted as in-channel and outwash sediments deposited during major floods. Matrix-supported cobble- and boulder-dominated lithofacies deposits commonly reflect mass transport and deposition as debris flow deposits (Bull 1972; Miall 1977, 1978). Clast-supported cobble and boulder gravel probably reflect tractional transport during aggradation of longitudinal bars (Miall 1977, 1978; Rust 1978).

Lithofacies Associations, Sedimentary Architecture, and Environments of Deposition

The architectural arrangement of lithofacies in the Ringold Formation on the Hanford Site is a complexly interstratified sequence of fluvial deposits composed of two principal lithofacies associations: coarse-grained channel deposits and fine-grained overbank and/or backswamp-lacustrine deposits. These sediments were deposited by both the ancestral Columbia and Salmon-Clearwater River systems as they crossed the Pasco Basin (Fecht *et al.* 1985). Fluvial deposits on the Hanford Site are stratigraphically complex and were subjected to numerous episodes of fluvial incision and pedogenesis. The intercalation and gradation between lithofacies seen in cross-sections and stratigraphic sections (Figures 5 and 10) are not easily reconciled by any existing lithofacies models (e.g., Rust and Koster 1984, Walker and Cant 1984, Collinson 1986).

Deposits of the coarse-grained channel lithofacies association are composed of lithofacies SS, SG, G, CB, and subordinate M and MS lithofacies. The abundance of coarse-grained lithofacies and the relative scarcity of mud-dominated lithofacies in this association suggest that deposition occurred primarily in a bedload-dominated stream system (see Schumm 1976, Galloway 1981). Deposits of this lithofacies association commonly display fining and coarsening upwards sequences that are less than 30 m thick (Figure 9). The fining-upwards sequences identified in our work are generally an order of magnitude thinner and much less continuous than those described by Webster and Crosby (1982).

Mapping the total thickness of coarse-grained lithofacies SS, SG, G, and CB in the Ringold Formation indicates that these lithofacies are concentrated in elongate trends (Figure 11). These coarse-grained lithofacies trends probably reflect multiple stacking of channel tracts that resulted from one or all of the following factors: 1) focusing of stream flow between Gable Mountain in the north and Yakima Ridge and Rattlesnake Mountain in the south, 2) lateral restriction of stream flow by highly cohesive mud-dominated overbank areas, and 3) structural controls. A high degree of vertical interconnectedness of such coarse-grained lithofacies is a common result of such channel stacking (Bridge and Leeder 1979).

The fine-grained overbank lithofacies association is composed of lithofacies M, MS, and subordinate SS. Deposits of this association commonly occur in highly dissected local sequences up to 50 m thick (Figure 5) and as relatively thin lenses and tongues. The fine-grained character and pedogenic alteration of lithofacies within this association support an overbank and/or backswamp-lacustrine interpretation.

The concentration of fine-grained lithofacies M and MS in relatively thick, but localized sequences (Figure 5) indicates that areas of fine-grained overbank deposition were stable for relatively long periods of time. Possible causes for such persistent deposition include: 1) restriction of depositional environments to structural lows and 2) the rapid accumulation of cohesive overbank muds. Thin lenses of lithofacies M and MS that intertongue with the coarser-grained lithofacies are common locally and are interpreted to reflect areas influenced by channel processes.

Discussion

Stratigraphic trends common to the Ringold Formation are not easily integrated into the generally used Ringold stratigraphic model (Myers *et al.* 1979, DOE 1988) because of the high degree of lateral and vertical variability of the component lithofacies of this unit. For example, where

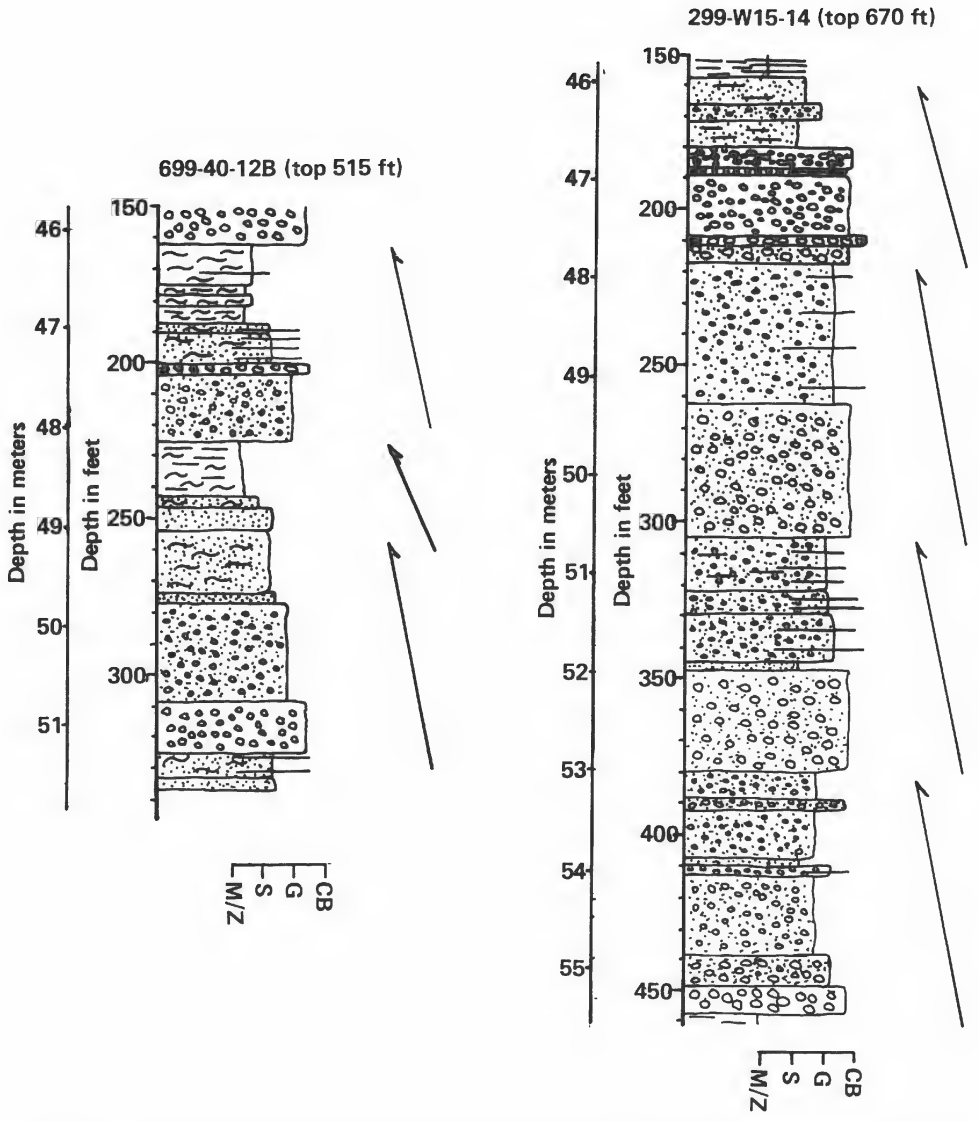

Figure 10. Fining-upwards fluvial sequences typical of those seen throughout the Ringold Formation. See Figure 12 for key to symbols.

multiple mud-dominated intervals are separated by thick, coarse-grained lithofacies (Figure 12), it is difficult, if not impossible, to determine the stratigraphic position of the lower mud-dominated unit. This problem is compounded further where strata typically assigned to the mud-dominated lower unit of Myers *et al.* (1979) grade into and intertongue with coarse-grained strata containing numerous fine-grained interbeds (Figure 5). In cases where fine-grained strata are absent (Figure 13), it often is not possible to differentiate between the gravels of the basal and middle units of the Ringold Formation.

It is generally accepted that syndepositional

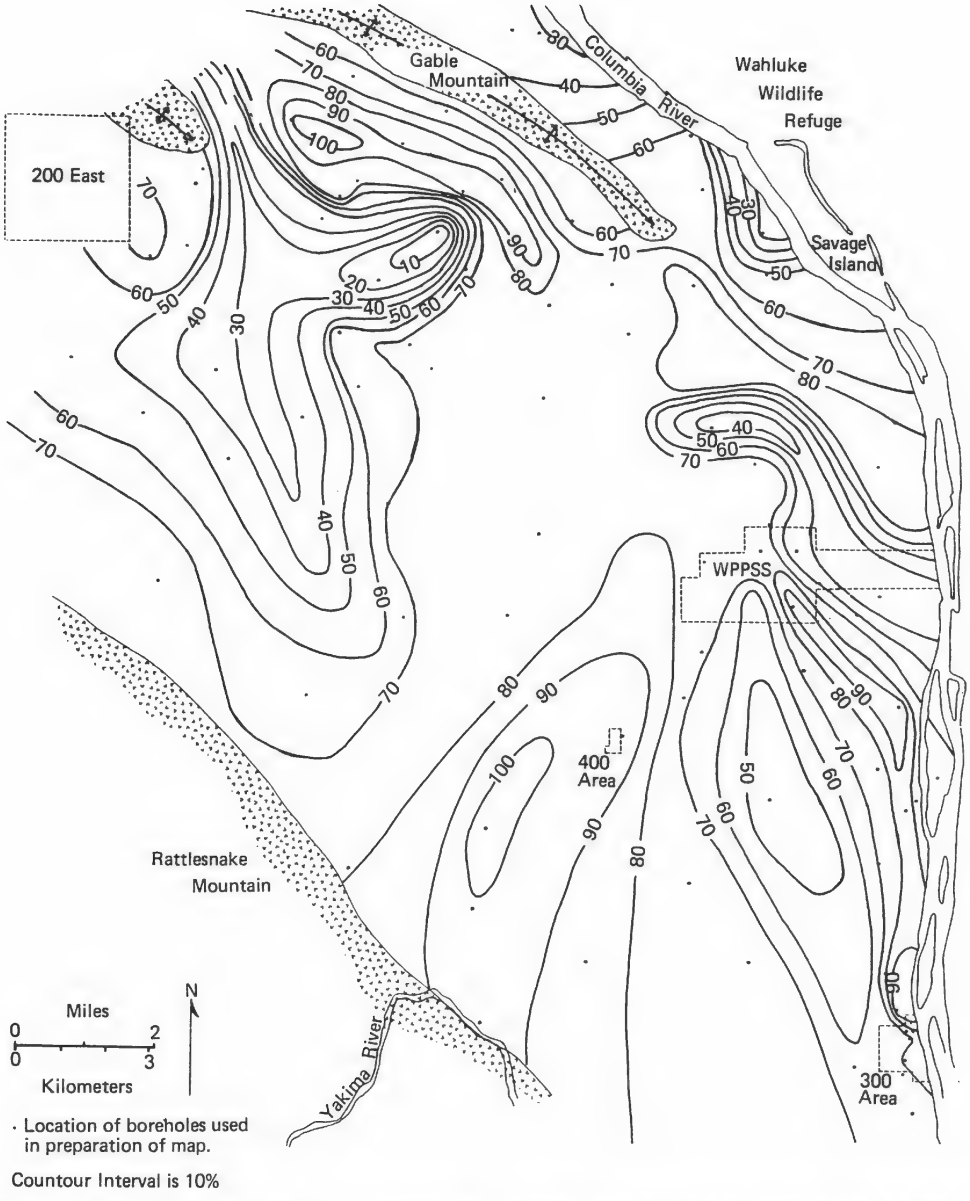

Figure 11. Map illustrating the distribution of coarse facies (SS, SG, G, and CB) in the Ringold Formation south of Gable Mountain. Contours indicate percent of coarse facies.

subsidence of the Pasco Basin influenced the position of fluvial depositional systems during accumulation of the Ringold Formation (Tallman *et al.* 1979, 1981; Reidel and Fecht 1981; Bjornstad 1985; Fecht *et al.* 1985; DOE 1988). For example, strata generally thicken into structural lows where subsidence and associated sedimentation are interpreted to have been more

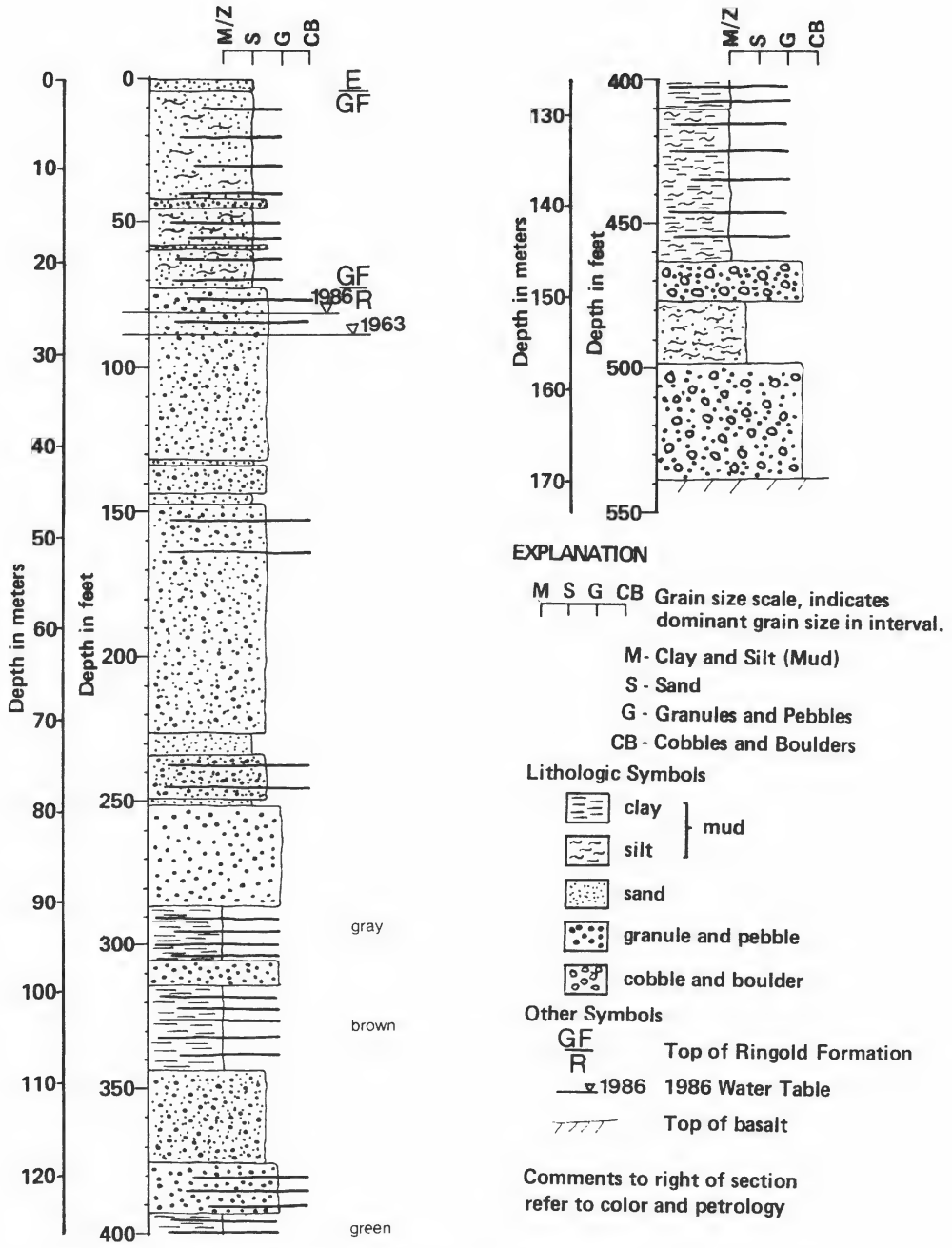

Figure 12. Geologic section of borehole 699-6-2A. This section shows a case where several mud-dominated facies are separated by thick gravelly strata.

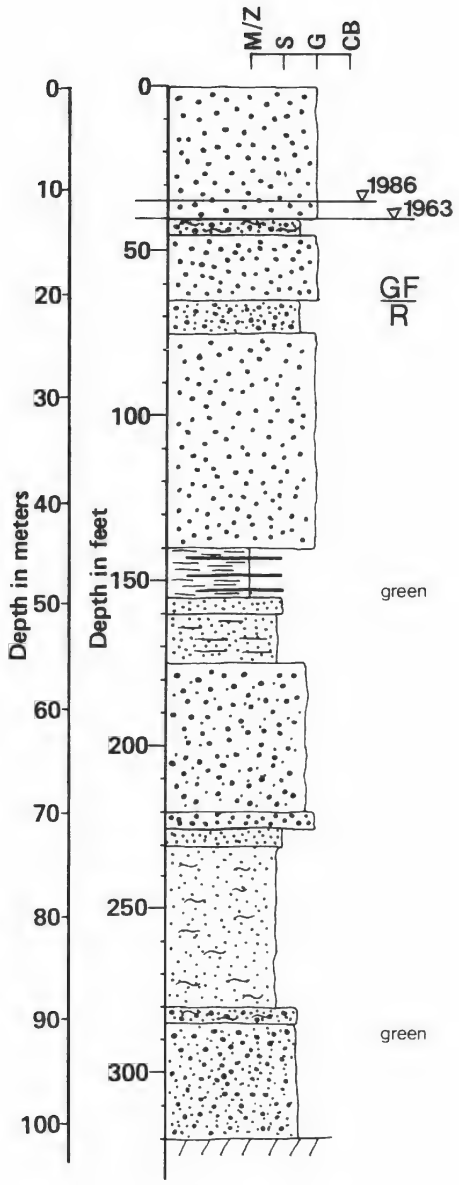

Figure 13. Geologic section of borehole 699-2-E14. This section demonstrates a case where mud-dominated strata largely are absent. See Figure 12 for key to symbols.

pronounced (Tallman *et al.* 1979, 1981; Reidel and Fecht 1981). Stratigraphic reconstructions completed as part of this work also indicate the importance of structural controls on sedimentation. However, there are cases where coarse-grained facies thicken onto structural highs (Figure 5) or sedimentation occurred transverse to a structural feature. Where this occurs sediment

distribution also was controlled by the migration of depositional environments within the fluvial system.

Conclusions

Analysis of existing subsurface geologic and geophysical data reveals that the five-tiered Ringold Formation stratigraphy as currently used at the Hanford Site may lead to erroneous interpretations of the distribution, architectural arrangement, and ultimately, geohydrologic properties of the Ringold Formation. In particular, the marked lenticularity and variability of Ringold strata, the relative lack of continuous marker horizons, and the gradational and ambiguous nature of unit contacts all hinder strict application of the generally accepted Ringold formation lithostratigraphic model (Myers *et al.* 1979, DOE 1988) to the Ringold Formation on the Site. An alternate method for the characterization of Ringold Formation strata has been suggested.

Six broad categories of lithofacies were defined primarily on the basis of grain size descriptions from geologic drill logs, textural analyses, and to a limited extent, on borehole geophysical logs, cores, and outcrops. These are: 1) mud (M), 2) mud and sand (MS), 3) sand (SS), 4) sand and granule to pebble gravel (SG), 5) granule to pebble gravel (G), and 6) cobble to boulder gravel (CB). These lithofacies aid in portraying the variability of sedimentary packages or elements, interpretation of depositional and erosional systems, and evaluation of hydrologic properties. The architectural arrangement of lithofacies in the Ringold Formation on the Hanford Site reveals a complexly stacked sequence of fluvial deposits composed of two principal lithofacies associations: coarse-grained channel deposits and fine-grained overbank and/or backswamp-lacustrine deposits. Coarse-grained channel deposits are concentrated along relatively elongate tracts reflecting multiple-stacking of bedload-dominated stream channel tracts. Overbank and/or backswamp-lacustrine deposits are concentrated in a few localized areas that escaped extensive stream channel incision for sedimentologic and structural reasons.

Acknowledgements

This research was supported by a grant to the Northwest College and University Association for Science (NORCUS) (University of Washington) for K. A. Lindsey by Westinghouse Hanford Company (WHC). NORCUS operates under Contract DE-AM06-76-RL02225 and WHC under Contract DE-AC06-87RL10930 with the U.S. Department of Energy. Additional support was provided to D. R. Gaylord by Battelle Pacific Northwest Laboratory under Contract B-N9191-A-6 with the U.S. Department of Energy. We wish to thank Bruce Bjornstad, Karl Fecht, Eileen Poeter, Mike Hagood, Steve Reidel, Ann Tallman, Tyler Gilmore, George Last, and Wally Walters for their useful discussions regarding Site geology and lithofacies. Review of this manuscript by Bruce Bjornstad, Steve Reidel, Jim Consort, Mike Hagood, Virginia Rohay, and Bob Peterson aided greatly in its preparation.

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Received 29 July 1989
Accepted for publication 20 December 1989

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Errata

WSU Press offers its sincere apologies to Jimmy L. Reaves, Charles G. Shaw, III, and John E. Mayfield, authors of "The Effects of *Trichoderma* spp. Isolated from Burned and Non-Burned Forest Soils on the Growth and Development of *Armillaria ostoyae* in Culture," which appeared in the February 1990 issue (Volume 64 Number 1) of *Northwest Science*. Due to a disk-write error that occurred during the final stages of production, the following errors were introduced into their article:

page 39, Abstract, line 2 should read "fire would alter the rhizosphere to favor the soil fungus *Trichoderma* spp. which has been shown to be strongly antagonistic"

page 41, column 1, line 13 should read "bark of a dead ponderosa pine tree near Bend,"

page 41, column 1, line 20 should read "dium which contained 30 g malt extract, 20 g dex-"

page 41, column 1, lines 40 and 41 should read "this suspension was added to a 500-ml Erlenmeyer flask containing 250 ml of liquid MEM and"

page 41, column 2, line 7 should read "of all filtrates of *Trichoderma* was adjusted to"

page 41, column 2, line 24 should read "scored for the presence or absence of rhizo-"

page 41, column 2, line 38 should read "followed by the Student Newman-Kuels multiple"

page 42, column 1, line 2 should read "sampled entry points in non-burned plots. Thus,"

page 42, column 1, line 4 should read "from either burned or non-burned soils were"

page 42, column 1, line 10 should read "or 60 days after burning was considerably greater"

page 42, column 1, line 20 should read "was *T. citrinoviride*)."

page 42, column 1, line 21 should read "TABLE 1. Recovery of *Trichoderma* isolates from soil pits"

page 42, column 2, line 49 should read "erally more inhibitory than those from"

Page 44, column 2, line 51 should read "Smith, R. S. 1984. Root disease-caused losses in commer-"

The authors were in no way responsible for these unfortunate mistakes.

—Managing Editor

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20-MILLION-YEAR-OLD DNA IN IDAHO

August 1990 Volume 64, Number 4

NORTHWEST SCIENCE

CONTENTS

Announcements

181 Evaluation of Rillscale for Herbivore Forage on Bentonite Mine Spoils—**Marguerite E. Voorhees and Daniel W. Uresk**

187 Estimating Demographic Rates of Long-Lived Trees—**Mark V. Wilson**

195 Movements, Habitat Use, and Spawning Strategies of Arctic Grayling in a Subalpine Lake Tributary—**David A. Beauchamp**

208 Cambrian and Upper Devonian Carbonate Lithologies of the Whitefish-MacDonald Range, Northwest Montana and Southeast British Columbia, A Preliminary Report—**W. Patrick Seward and Larry E. Davis**

219 Lead and Cadmium Concentrations in Mink from Northern Idaho—**Lawrence J. Blus and Charles J. Henny**

224 Effect of Substrate Composition and Stock Origin on the Survival to Emergence of Brown Trout: A Laboratory Study—**Michael K. Young, Wayne A. Hubert, and Thomas A. Wesche**

232 Research News and Comments: "The Clarkia "Fossil" Leaves: Windows to the Past"—**David E. Giannasi**

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CONTENTS

Announcements

181 Evaluation of Rillscale for Herbivore Forage on Bentonite Mine Spoils—**Marguerite E. Voorhees and Daniel W. Uresk**

187 Estimating Demographic Rates of Long-Lived Trees—**Mark V. Wilson**

195 Movements, Habitat Use, and Spawning Strategies of Arctic Grayling in a Subalpine Lake Tributary—**David A. Beauchamp**

208 Cambrian and Upper Devonian Carbonate Lithologies of the Whitefish-MacDonald Range, Northwest Montana and Southeast British Columbia, A Preliminary Report—**W. Patrick Seward and Larry E. Davis**

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224 Effect of Substrate Composition and Stock Origin on the Survival to Emergence of Brown Trout: A Laboratory Study—**Michael K. Young, Wayne A. Hubert, and Thomas A. Wesche**

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Announcements

Fossilized bones and teeth and shells are the customary hard parts that preserve the record of animals now extinct. Fossilized tree trunks and impressions of their leaves sometimes survive to give us a look at the plants that shared the earth with animals millions of years ago. But for most scientists, the genetic code of life, the DNA, was thought to have perished along with the other soft parts. As technology and opportunity improved, many began to realize that all was not so hopeless, and just a few months ago a sequence of DNA from a 20-million-year-old *Magnolia* was described. The story of that work, discovery of the specimen, the wait for the technology to catch up, and the excitement of the finished work is told by one of the participants, Dr. David Giannasi from the University of Georgia, in a charming short piece appearing at the end of this issue.

My thanks go to Dr. Giannasi for quickly responding to our request for a short background piece on the work.

—Editor

Marguerite E. Voorhees and **Daniel W. Uresk,** USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Rapid City, South Dakota 57701

Evaluation of Rillscale for Herbivore Forage on Bentonite Mine Spoils

Abstract

The forage quality of rillscale (*Atriplex suckleyi*), a native annual species, was evaluated to assess its potential as herbivore forage on bentonite mine spoils. Production estimates were 3432 kg/ha with spoil treatment. Seasonal growth trends and forage quality indicate that rillscale has favorable nutritional qualities for large herbivores. Forage quality was respectable, with dry matter digestibility ranging from 56 percent to 80 percent. Metabolizable energy was 2.51 Mcal/kg and crude protein ranged from 5 to 12 percent. Data for eighteen elements that affect forage quality are presented. These show that rillscale has the capability for making a substantial contribution to the nutrition of large herbivores, although the potential exists for imbalances of iron, magnesium, and zinc.

The major bentonitic deposits in the United States occur in the three-state region of Montana, Wyoming, and South Dakota (Solomon 1973). Most deposits in South Dakota have been depleted and reserves in Wyoming are relatively limited. Montana will experience most intensive development of bentonitic deposits in the next 20 years.

The areal extent of disturbance as a result of bentonite mining is much greater than is generally realized. Disturbance appears to be limited because of the small size (1 to 4 ha) and wide dispersal of pits. A statistical compilation for the state of Montana in 1978 revealed that bentonite mining ranked with coal mining in areal extent of disturbance (Solomon 1973); however bentonite mine spoil, which is sodic, is much more difficult to reclaim (Uresk and Yamamoto 1986, Smith *et al.* 1985, Voorhees *et al.* 1983, Voorhees *et al.* 1987, Sieg *et al.* 1983a).

Industry efforts to comply with reclamation regulations generally include grading, covering with topsoil, and seeding to several plant species conventionally used in reclamation of other types of spoil. There is typically very little vegetative establishment despite these efforts because on most sites salt eventually migrates from spoil to contaminate the soil.

The Forest Research Laboratory in Rapid City has been involved in research on rehabilitation of bentonite mine spoil since the early 1970's. A study to explore and develop the potential of the primary native invader of spoil, rillscale (*Atriplex suckleyi*), was initiated in 1981 after essential failure of several drought- and saline-tolerant plant species in field trials on abandoned spoil (Uresk and Yamamoto 1986).

Rillscale, a native annual, is a member of a genus valued by range managers, i.e., *Atriplex.* Perennial *Atriplex* species have high forage value (digestibility, protein, palatability, etc.), and some annual species have been cultivated as hay crops. Wildlife and domestic livestock commonly utilize plants of this genus (Shoop *et al.* 1985, Sieg *et al.* 1983b). Herbivore use is the major proposed post-reclamation land use in bentonite-mined regions. Therefore, selection of nutritious and palatable plants is important.

The objectives of this study were to determine productive capabilities, seasonal availability, and forage quality of rillscale. Observations on these parameters are discussed in this paper and incorporated into recommendations for management.

Study Area and Methods

The study area was west of the Black Hills on the Mowry Shale formation in northeastern Wyoming, approximately 2 km northwest of Upton. Sites on the property had been mined at various times during a period of more than 30 years. Elevation at the study area was approximately 1290 m. Average annual precipitation is about 370 mm (National Oceanic and Atmospheric Administration 1983), with 75% received during the growing season from April to September (Thornburg and Fuchs 1978). Vegetation is characteristically big sagebrush (*Artemisia tridentata*) grassland (predominantly *Agropyron smithii* and *Bouteloua gracilis*) interspersed with

stands of ponderosa pine (*Pinus ponderosa*). The area provides forage for livestock and habitat for many species of wildlife, including antelope (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*).

Plots on Raw Spoil

Three sites (replications) were selected on raw spoil in order to characterize biomass and chemical composition of the foliage of rillscale. These sites were selected for level topography and geological uniformity. One 50-m transect was located on each site at random. Aboveground biomass was collected by clipping plants near the spoil surface from ten 0.2-m^2 quadrats located at 5-m intervals along each transect comprising a total of 30 plots. Quadrats were moved forward 1-m along the transect at each of five sampling dates at equal intervals throughout the growing season so that no quadrat was sampled more than once. Plant tissue samples from each transect were composited for estimation of standing crop and for chemical analyses. Height of the tallest plant within three 10-cm^2 quadrats in each of ten 1-m^2 permanent circular plots at equally spaced intervals along each transect was measured at the first three sampling dates.

Plots on Treated Spoil

Culturally treated plots were established on raw spoil in order to assess productive capabilities of rillscale on soils treated with amendments known to have significant positive effects on its growth (Vorhees *et al.* 1987). Gypsum (31 Mg/ha), inorganic chemical nutrient (114 kg/ha N, 23 kg/ha P, 50 kg/ha K), and wood residue (48 mt/ha with 6% added nitrogen) amendments were all applied to each of three tilled plots that were 60 x 150 cm in size. Aboveground biomass was harvested from half of each plot during early July 1983 and from the other half during mid-August for estimation of standing crop. Plant tissue collected from each plot in early July 1983 was used in chemical analyses. Maximum plant height of rillscale in each of five 10-cm^2 quadrats located at 10-cm intervals along a transect of each plot was measured to the nearest centimeters.

Chemical Analyses

Plant tissue was oven-dried at 55°C, weighed, and ground through a 20-mesh screen. Plant tissue analyses included total nitrogen by conventional micro-Kjeldahl, in vitro dry matter digestibility (Tilley and Terry 1963), and percentage ash (A.O.A.C. 1985). Crude protein percentage was estimated from Kjeldahl nitrogen (CP = N% x 6.25).

Elemental concentrations of nitric acid-extractable aluminum, arsenic, barium, boron, calcium, chromium, copper, iron, magnesium, manganese, molybdenum, nickel, phosphorus, potassium, selenium, sodium, strontium, titanium, and zinc were determined for the plant tissue by using inductively coupled plasma atomic emission spectrometry (ICP-AES) (Fassel and Knisely 1974, Jones 1977, Havlin and Soltanpour 1980, Gestring and Soltanpour 1981).

Statistical Analysis

Mean maximum plant height of rillscale for each treated plot was calculated from the five height measurements, whereas mean maximum plant height for each transect on raw spoil was calculated from values recorded for each of ten quadrats ($n = 3$). Quadrats where no plants were found were excluded from calculations of mean maximum plant height. Standing crop, plant height, and plant tissue compositional parameters of each plot on treated spoil were compared with similar variables for transects on adjacent raw spoil using either a separate or a pooled t-test, as dictated by variance homogeneity ($n = 3$). Box's approximation for evaluating the significance of Bartlett's test was used to evaluate variance homogeneity (Dixon and Massey 1969). Equality of each foliage compositional parameter among treatment dates on raw spoil was tested using classical one-way analysis of variance (F-statistic) when variances were found to be equal using Levene's test. Parameters with unequal variances were tested using statistics that do not assume equality of variances, i.e. Welch and Brown-Forsythe statistics (Brown and Forsythe 1974). Differences were accepted as significant at $p \leq 0.05$.

Results and Discussion

Rillscale is an annual and consequently was expected to have limited seasonal growth and availability due to rapid drying and fragmentation that follow maturity in mid-summer. Figure 1 illustrates the rapid rise and even more rapid

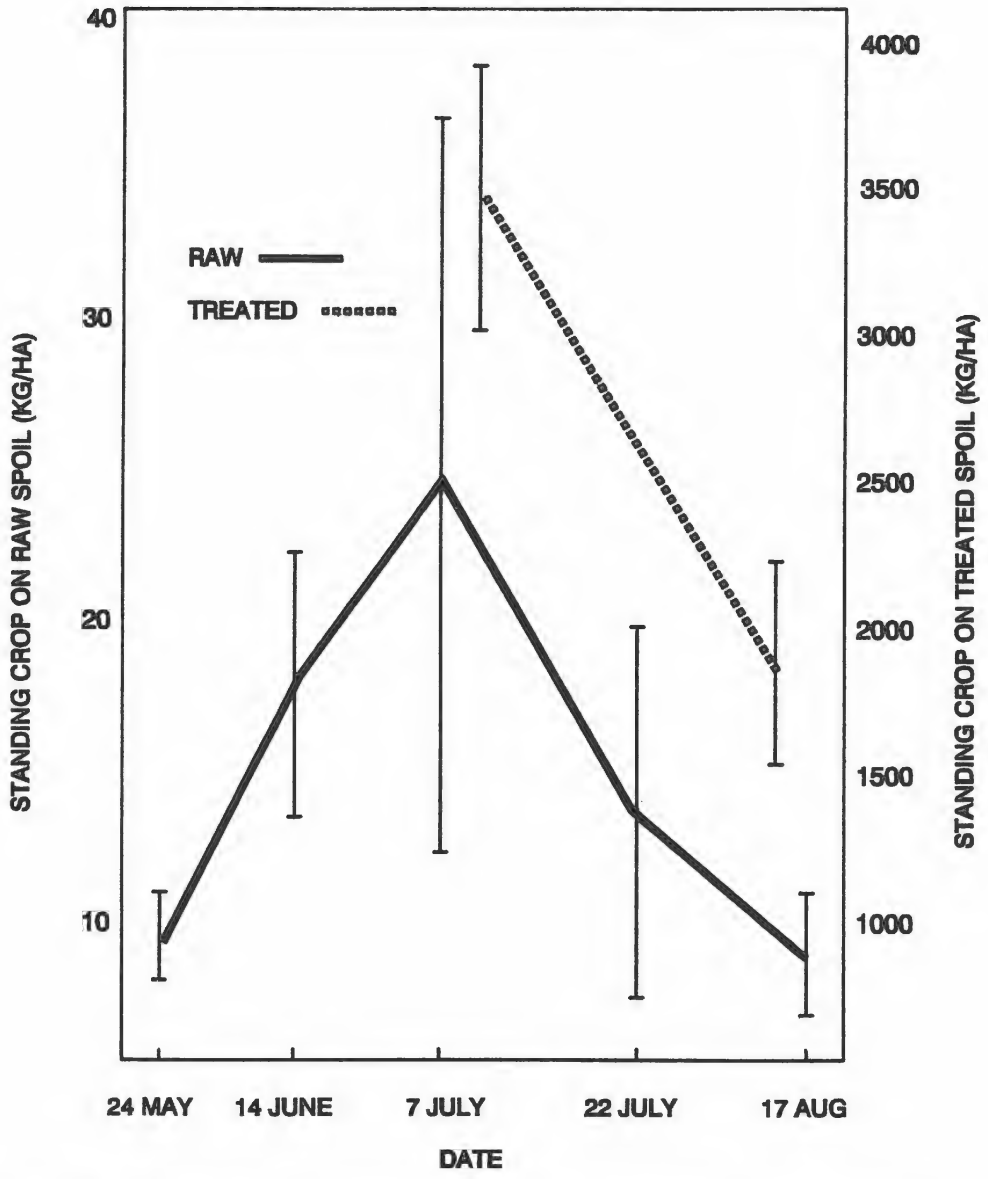

Figure 1. Seasonal growth trends for rillscale grown on raw and treated bentonite spoil with ± standard error bars.

decline in standing crop of rillscale grown on raw spoil. Peak standing crop (production) on raw spoil (26 kg/ha) was low. Plant heights (Table 1) on raw spoil were near or below the minimum required for substantial utilization by large herbivores, throughout the growing season (Bjugstad and Whitman 1970).

Rillscale exhibited greatly escalated growth with cultural treatment. Production on treated spoil (3432 kg/ha) was greater than the production of tallgrass prairie under favorable conditions (3300 kg/ha) (Stoddart *et al.* 1975) and

TABLE 1. Mean maximum plant height (cm) of rillscale on raw spoil and on treated spoil at three sampling dates during the 1983 growing season.

Spoil type	Date		
	24 May	14 June	7 July
Raw	1.4a[1]	2.4ab	3.5b
Treated	6.6a*	11.7b*	12.5b*

[1]Height values within a spoil type followed by the same letter are not significantly different at $p \leq 0.05$.

*Height values on treated spoil are significantly different from height values on raw spoil on the same date ($p \leq 0.05$).

exceeded critical bite size (Minson 1951) by over 133 percent. Height of plants on treated spoil was adequate for use by cattle on all sampling dates (Table 1). Extrapolation of seasonal growth trends on raw spoil to production on amended spoil (Figure 1) indicated that significant amounts of forage would be available for a minimum of 4 to 6 weeks during favorable years, beginning in early to mid-June and terminating in mid-July if spoil were treated. The period during which adequate forage would be available on treated spoil would actually be longer, because the rate of decline in measured standing crop on treated spoil was significantly lower than on raw spoil.

Rillscale demonstrated acceptable forage quality characteristics (Table 2). Energy and digestibility were high with respect to other common range forages. Digestibility ranged from 56 percent to nearly 80 percent. Metabolizable energy, as estimated from DMD (Rittenhouse *et al.* 1971) for purposes of comparison, was as high as 2.51 Mcal/kg on raw spoil and was increased nearly 20 percent by spoil treatment ($p \leq 0.05$). Alfalfa (*Medicago sativa*) is rated as high as 2.28 Mcal/kg metabolizable energy and 71% dry matter digestibility (National Research Council 1984). The protein content of rillscale (5-12%) was comparable to many range forages.

Rillscale foliage grown on treated spoil had a high salt content as indicated by an average ash content that ranged from 35 percent to 46 percent over the growing season. Sodium content was as high as 7 percent on raw spoil. Such a high sodium content is to be expected as *Atriplex* species generally compensate for a highly saline substrate by accumulating salts. Foliage grown on treated spoil was higher ($p \leq 0.05$) in sodium at 7.8%.

More serious forage quality liabilities of rillscale included potentially toxic levels of iron (as much as 24,900 μg/g), manganese (as much as 2555 μg/g), and aluminum (as much as 4350 μg/g) (Table 2). Iron levels of 100 to 2500 μg/g have been suggested as the lower limit of toxicity for cattle depending on the availability of iron in the particular diet. One thousand μg/g is the maximum tolerable level of aluminum and manganese indicated by the National Research Council for cattle (National Research Council 1984).

High dietary levels of iron as ferrous sulfate have been associated with decreased plasma phosphorus and decreased performance in steers (McDowell 1985). Aluminum toxicity has been implicated as a cause of tetany and phosphorus deficiency (Alfrey 1986).

Manganese is considered the least toxic trace mineral for animals. Decreased feed intake and decreased body weights were associated with a manganese supplemented raion of 2460 ppm and above. Sheep showed similar effects at lower concentrations of dietary manganese (Hurley and Keen 1986).

Mutual antagonism between iron and manganese at the level of absorption may decrease the adverse effects of either. High levels of some elements may have been a result of contamination with spoil material.

The ratio of copper to molybdenum in foliage was adequate on raw spoil at 3.3 to 4.8, but was very much lower ($p \leq 0.05$) on treated spoil at 0.3, which could cause molybdenosis in animals. Molybdenum induced copper deficiencies, expected to occur at copper to molybdenum ratios below 2.0 (Miltmore and Mason 1971), have been documented in this region. Rillscale has been shown to be a molybdenum accumulator (Voorhees, unpublished data), but problems with high molybdenum content of bentonite spoil are probably localized.

Rillscale produced considerable quantities of forage and had valuable forage quality characteristics. Although some potential for elemental toxicities and imbalances exists, these would not develop unless unlikely conditions of intensive, exclusive, and prolonged use of rillscale occurred. Intensive and exclusive use would be unlikely because of the small size (1 to 4 ha) and wide

TABLE 2. Standing crop and chemical composition of the foliage of rillscale grown on raw bentonite mine spoil at five sampling dates during 1983.

	Raw Spoil					Treated Spoil
	Date					
Property (units)	24 May	14 June	7 July	22 July	17 Aug.	7 July
Standing crop (kg/ha)	7ab[1]	18ab	26b	11ab	4a	3432*
Dry matter digestibility (%)	71b	79b	59a	60a	56a	71
Crude protein (%)	12c	10bc	8abc	5a	6ab	13
Ash (%)	36a	35a	40ab	45b	46b	34
Ca (%)	0.49a	0.47a	0.56ab	0.70b	0.70b	0.48*
Mg (%)	1.28a	1.41a	1.25a	1.21a	1.22a	0.83
P (%)	0.31c	0.27bc	0.11a	0.12a	0.17ab	0.16
Na (%)	6.36bc	7.01c	5.16ab	3.94a	4.80ab	7.76*
K (%)	1.80a	1.59a	1.42a	1.13a	1.11a	1.04
Zn (μg/g)	92ab	85a	104ab	129b	101ab	65
Fe (μg/g)	8345a	5930a	17000b	22000bc	24900c	10350
Mn (μg/g)	479a	371a	1280ab	2555b	1633ab	423
Ni (μg/g)	16a	16a	18a	29a	17a	7*
Cr (μg/g)	5ab	4a	8bc	12d	8c	7
Cu (μg/g)	10ab	7a	13abc	17c	12bc	6*
Mo (μg/g)	2a	2a	3ab	6b	3ab	24
B (μg/g)	39ab	49b	27a	33ab	30ab	43
Al (μg/g)	3120b	1357a	2825ab	4350b	3360b	1370
Ba μg/g)	55a	25a	22a	75a	81a	52
Sr μg/g)	49a	42a	70ab	116b	108b	100*
Ti μg/g)	8ab	6a	5a	12b	7a	10
Cu:Mo	4.75a	3.50a	4.17a	3.31a	4.72a	0.28*

[1]Values for a given parameter within a spoil type that are followed by a similar letter are not significantly different at $p \leq 0.05$.

*Values for a given parameter on treated spoil are significantly different from similar parameters of foliage on raw spoil on the same date ($p \leq 0.05$).

dispersal of pits over the region. Animals do not appear to selectively seek rillscale though they have been observed to utilize it as forage. Prolonged use would be unlikely because of the relatively short periods of time during which rillscale is available as forage. Assessment of the composition of the diets of wildlife and livestock that forage on these areas would be prudent and useful to determine palatability and toxic potential. Theoretically other plant species could be planted with rillscale (Uresk and Yamamoto 1986, Welch 1989) to further decrease the possibility of dietary imbalances and toxicities although results of previous field trials utilizing other species indicate practical limitations to this approach.

Conclusions

Rillscale has potential for use in revegetation of spoil and for use as forage. This plant demonstrated a capability for making a substantial contribution to the nutrition of large herbivores, especially when spoil treatments were applied. However, the potential for toxicities and imbalances of rillscale for herbivores may exist for iron, manganese and aluminum. High concentrations of these elements may reflect spoil contamination of foliage. Foliage samples were not washed in order that they might more truly represent what would be ingested by a foraging herbivore. Native forage on undisturbed areas adjacent to spoil might be a potential hazard as well if this is the case. This possibility deserves investigation because it represents a potential loss in grazing value that perhaps has not been considered. Although the degree of rillscale consumed is unknown, cattle and deer have been observed by the authors to utilize rillscale as forage.

Acknowledgments

Thanks are extended to Joe Trlicia, Department of Range Science, Colorado State University, Ft. Collins, CO for his helpful suggestions throughout the study. American Colloid provided study areas.

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Received 12 May 1989
Accepted for publication 6 February 1990

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Estimating Demographic Rates of Long-Lived Trees

Abstract

Long-lived species, such as many Pacific Northwest trees, pose special problems for studies in demography. A demographic model is presented that combines knowledge of current age distribution with detailed information of past environmental conditions gained from stand reconstruction techniques. The model makes simple assumptions about the influence of environmental factors on year-to-year survivorship. Multiple regression analysis then allows the direct estimation of birth rates and age-specific and environment-specific survival rates for the population. This new analytic tool should be useful for investigating environmental control of tree population dynamics.

Introduction

Birth and death rates provide basic information about populations. When these rates are specific to age and environment, they encapsulate much of the dynamics of a population and help reveal the mechanisms controlling population size. Unfortunately, most methods for estimating demographic parameters, including cohort and current life table analysis, are inadequate for studying the long-lived tree species common in the Pacific Northwest. Current (static) life tables are constructed from short-term observations of the births and deaths of an entire, multi-aged population. Demographic rates estimated from the analysis of current life tables are valid only if the age distribution of the population is stationary (Pielou 1977), but this condition seldom holds for field populations responding to a changing environment. Constructing cohort life tables, on the other hand, requires following individuals born within the same time interval throughout each of their lifetimes. Thus, only short-lived organisms are suitable for study as cohorts (e.g., Leverich and Levin 1979, Mack and Pyke 1983, Silvertown 1985).

The goal of this paper is to present a new method of demographic analysis suitable for the study of long-lived trees. The method combines information on a population's current age structure with reconstruction of past environmental conditions to produce estimates of birth rates and age-specific and environment-specific survival rates.

Model Development

Consider a general demographic model of the survivorship of a long-lived species:

$$N_x = N_0 \bullet S_1 \bullet S_2 \bullet \ldots \bullet S_x \qquad (1)$$

where N_0 is the total number of individuals born in a certain time interval, N_x is the number alive of age x, and each S_i is the proportion surviving from age class i-1 to i. The relative values of N_x for a population at a particular time describes its age structure. The units of x could be single years, 5 years, or another convenient interval.

The actual age-specific survival rates (S_i) result from the interaction of the population's potential or inherent age-specific survival under optimal environmental conditions with the constraint imposed on survival by an unfavorable environment. For a single environmental factor j, this relationship between population potential and environmental constraint can be described as

$$S_i(t) = \hat{S}_i \bullet C_{ij}(t) \qquad (0 \leq C_{ij}(t) \leq 1) \qquad (2)$$

where $S_i(t)$ is the actual survival rate for age class i at time t, $\hat{S}_i$ is the potential survival rate for age class i, and $C_{ij}(t)$ is the constraint imposed on survival of age class i by the environmental factor at time t. The constraint on survival is larger when $C_{ij}(t)$ is smaller; for example, $C_{ij}(t) = 1.0$ means that survival is not reduced by the environmental condition. It is useful to define $e_j(t)$ as the effect on survival of environmental factor j at time t. Then the relative favorableness ($F_j(t)$) of factor j at time t is

$$F_j(t) = \frac{e_j(t)}{\max e_j},$$

where $e_j(t) \geq 0$ and max e_j is the most favorable state in which factor j occurs. (The relationship between environment and favorableness, as depicted in the e_j values, ideally should be determined from prior studies.) A simple, albeit

arbitrary way to relate relative favorableness (F) to environmental constraint (C) on survival is

$$C_{ij}(t) = F_j(t)^{\beta ij} \qquad (\beta \geq 0) \tag{3}$$

where β_{ij} is a parameter specific for age class i and environmental factor j. With this power-function form, different values of the single parameter in equation 3 (β) allow the relationship between environmental favorableness and constraint to range between severe constraint on survival under any suboptimal conditions (β very large) to no constraint under any environmental condition ($\beta = 0$) (Figure 1).

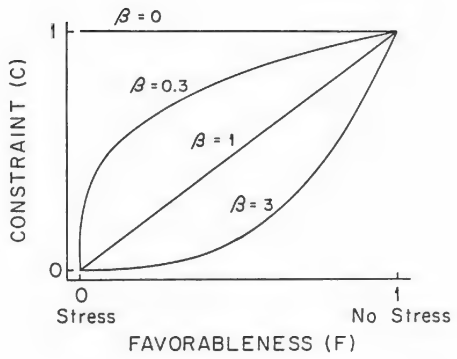

Figure 1. The relationship between relative environmental favorableness and constraint on survival rates described by equation 3. Large values of C mean that the survival rate is close to the rate that would occur under optimal environmental conditions. The shape of the relationship depends on the value of β. If β is large, then unfavorable conditions strongly decrease survival. If $\beta = 0$, survival is unaffected by the state of the environmental factor.

Field populations, of course, are influenced by more than one environmental factor at a time. Moreover, exposure to one stress can sometimes predispose or harden a plant to another (Levitt 1980). Nevertheless, a useful first approximation is to assume that constraints on survival of multiple environmental factors act independently of one another. Under this assumption, the overall environmental constraint ($C_i(t)$) on the survival of age class i is

$$C_i(t) = C_{i1}(t) \bullet C_{i2}(t) \bullet \ldots \bullet C_{iv}(t) \tag{4}$$

$$C_i(t) = \prod_{j=1}^{v} C_{ij}(t)$$

where v is the total number of environmental factors being described. Substituting into equation 4 the relationship between single environmental factors and constraints on survival described in equation 3 produces

$$C_i(t) = \prod_{j=1}^{v} F_j(t)^{\beta ij}. \tag{5}$$

The extension of equation 2 for the case of several environmental factors is then

$$S_i(t) = \hat{S}_i \prod_{j=1}^{v} F_j(t)^{\beta ij}. \tag{6}$$

At this point, the general demographic model described in equation 1 can be rewritten to include the constraints on survival developed in equations 2 through 6:

$$N_x(t) = N_0(t\text{-}x) \prod_{i=1}^{x} S_i(t\text{-}x+i) \tag{7a}$$

$$N_x(t) = N_0(t\text{-}x) \prod_{i=1}^{x} \left\{ \hat{S}_i \prod_{j=1}^{v} F_j(t\text{-}x+i)^{\beta ij} \right\}. \tag{7b}$$

Equation 7b describes the expected number of individuals of age x at time t that had experienced a particular sequence of environmental conditions. This sequence corresponds to a time series of variables F_j. For example, for j = 2 environmental factors, a sequence of environmental conditions over three time periods can be written as

$$\{F_1(t\text{-}2), F_2(t\text{-}2)\},\ \{F_1(t\text{-}1), F_2(t\text{-}1)\},\ \{F_1(t), F_2(t)\}.$$

Different environmental histories would have different sequences of F values. Many of these sequences would undoubtedly be necessary to account for the heterogeneous environmental histories of most ecosystems. Thus, the final demographic model is actually a series of equations, each of the form shown in equation 7b. Each equation describes the relationship between a unique temporal sequence of environmental conditions (seen in the different values of F_j through time) and the number of individuals alive of age x ($N_x(t)$) that have lived through the environmental sequence. Although each equation differs in the values of the independent variables (the F_j) and the dependent variables (the N_x values), they partially share some parameters (the N_0, $\hat{S}_i$, and β_{ij} values).

The number of equations in the final model is potentially very large. For x = 1 (the first age class), the number of unique environmental sequences would be the number of distinct, current environmental conditions (v). For older age

classes ($x > 1$), the possibility of permutations of different environmental conditions occurring in different sequences over time means that the potential number of unique sequences is substantial ($= v^x$). In practice, however, most sequences will not occur. For example, litter depth in forests should increase steadily through time except for occasional, rapid consumption by fire. Irregular fluctuations in litter depth are improbable and the actual number of unique environmental sequences in this example would be much less than the potential number.

Application

The use of the final model in demographic analysis requires relating the information on the current tree age structure ($N_x(t)$) with past environmental conditions. The first step in field application is to divide the study area into patches or quadrats that have the same environmental history. Estimates of the actual past environmental conditions are best derived from stand reconstruction techniques (e.g., Henry and Swan 1974, Oliver and Stephens 1977, Lorimer 1985, Kelty 1986, Larson 1986). Stand reconstruction uses current evidence to infer past environmental events and conditions. For example, fire scars on trees can be used to date and estimate the extent of a past fire and the concomitant changes in light conditions, soil chemistry, and understory competition. To be useful for demographic analysis, stand reconstruction must yield information on the past environment of each sample quadrat. Then the sample quadrats can be placed into groups having identical sequences of past environmental conditions.

The next step requires the translation of environmental conditions into degrees of favorableness (e_j). This conversion must stem from prior studies of the species's mortality response to the environment. For this model, only a few, arbitrary categories of favorableness need to be identified.

The dependent variables in the final model are the series of values representing the number of individuals alive at different ages (the N_x values) that had experienced the same sequence of environmental conditions. These values are obtained by aging and counting individuals occurring in quadrats having the same sequence of environmental conditions.

The values of $F_j(t\text{-}x+i)$ and $N_x(t)$ are then substituted into the series of equations constituting the final demographic model. In the final demographic model, exemplified by equation 7b, there are enough equations to estimate all but one of the parameters. The best solution to this problem is to assume that population birth rates are constant through time: $N_0(t) = N_0$ for all t. This assumption is decidedly poor for most trees if the time intervals are years: mast seeding years in trees are well documented. With longer time intervals, such as 10 years, the assumption of constant population birth rate is much more reasonable. A related characteristic of the model is that birth rates (N_0) cannot be distinguished from first year potential survival rate ($\hat{S}_1$). That is, the method estimates $N_0 \cdot \hat{S}_1$, the number of new seedlings alive at the end of the first age interval under optimal environmental conditions.

The series of equations constituting the final demographic model can be solved by nonlinear regression for the unknown parameters: $N_0 \cdot \hat{S}_1$, the number of new seedlings alive at the end of the first age interval under optimal environmental conditions; $\hat{S}_2, \hat{S}_3, \ldots, \hat{S}_x$, the potential age-specific survival rates; and the β_{ij} values, the coefficients indicating the constraint of environmental factor j on the survival of age class i.

Hypothetical data can help illustrate the method. Consider a tree species with a 90 yr life span growing in a 1 ha forested study area (Table 1). (The short, 90 yr life span was chosen to simplify the hypothetical example. The model can accommodate longer time spans if past environmental conditions can be reconstructed.) In this example, precipitation data are available for the 90 yr time span from 1901 to 1990. Precipitation data coupled with data on soil and topographic affects on water availability allow construction of a quadrat-by-quadrat moisture index for the 30 yr intervals since 1901. Other ecological studies of this hypothetical tree species showed that, in general, abundant water was most favorable for tree survival. That is, drought stress leads to tree death. Stand reconstruction within quadrats revealed past conditions of basal area (the total area of ground covered by trees measured at breast height) during 30 yr intervals from 1901 to 1990. Prior ecological studies of this hypothetical tree showed that the high light environment under sparse canopies associated with low stand basal area was generally favorable

for tree survival. Analysis of all quadrats showed six unique sequences of environmental conditions. Tree density (Table 1) ranged between 261.7 individuals/100 m^2 (in the 0 to 30 yr age class undergoing environmental sequence 1) and 1.1 individuals/100 m^2 (in the 60 to 90 yr age class in sequence 4).

Nonlinear regression of population densities against relative favorableness in this hypothetical example produced estimates of the parameters of equation 7b (Table 2). (Details of the solution procedure are presented in the appendix.) This example also shows the types of ecological interpretations possible based on results from the demographic analysis. For example, potential survival rate increased from the second age class (0.46) to the third (0.99), suggesting that adults face fewer hazards than juveniles. Basal area had little effect on survival of the first age class (β_{11} = 0.26). One hypothesis accounting for this result is that, for tree seedlings, the negative effect of reduction in light is compensated for by the positive effect of the reduction in drought stress caused by high canopy cover. In contrast, unfavorable light conditions strongly reduced the survival of age class two (β_{21} = 1.51). Water availability (represented by the moisture index) showed the opposite pattern. The high value of

TABLE 1. Hypothetical field data of the type needed for application of the demographic model. The environmental sequences are six unique temporal patterns of basal area (BA) and a moisture index (MI) over the period 1901-1990. Population density is the number of tree individuals currently alive that have experienced a particular sequence of environmental conditions. This hypothetical example presents densities for three age classes.

Environmental sequence (es)	Relative favorableness 1901-30 BA	1901-30 MI	1931-60 BA	1931-60 MI	1961-90 BA	1961-90 MI	Population density (individuals/100m^2) 0-30 yr	30-60 yr	60-90 yr
es_1	1	0.6	0.6	1.0	0.5	0.7	261.7	60.6	27.3
es_2	0.8	0.5	0.8	0.8	0.6	0.6	214.8	59.5	27.1
es_3	0.8	0.5	0.5	0.8	0.2	0.6	161.5	10.1	7.7
es_4	0.2	0.3	0.4	0.5	0.2	0.4	96.2	3.9	1.1
es_5	0.8	0.5	0.7	0.8	0.4	0.6	191.1	31.7	18.1
es_6	0.3	0.4	0.3	0.6	0.3	0.4	105.2	8.5	1.6

TABLE 2. Results of nonlinear multiple regression of the hypothetical tree data in Table 1.

Parameter	Meaning	Estimate	t
$N_0 \cdot \hat{S}_1$	New seedlings alive at the end of the 1st age interval under optimal conditions	504.5/100 m^2	46.0*
$\hat{S}_2$	Potential survival rate during the 2nd age interval under optimal conditions	0.46	5.4*
$\hat{S}_3$	Potential survival rate during the 3rd age interval under optimal conditions	0.99	1.9
β_{11}	Effect of basal area on 1st age interval survival	0.26	13.8*
β_{21}	Effect of basal area on 2nd age interval survival	1.51	9.0*
β_{31}	Effect of basal area on 3rd age interval survival	0.50	1.7
β_{12}	Effect of moisture index on 1st age interval survival	1.39	29.5*
β_{22}	Effect of moisture index on 2nd age interval survival	0.42	1.3
β_{32}	Effect of moisture index on 3rd age interval survival	0.82	0.8

*$P < .05$

β_{12} (1.39) suggests strong reduction of survival because of drought stress in the first age class. The lower and statistically nonsignificant value of β_{22} (0.42) and β_{32} (0.82) suggests that older tree individuals are less susceptible to drought stress, perhaps because of their more extensive roots. Hypotheses stemming from this demographic analysis could be tested by subsequent, more specific studies.

Discussion

The demographic analysis described here uses information derived from stand reconstruction combined with models of population dynamics to derive birth rates and age-specific and environment-specific survival rates. In effect, the method approximates a longitudinal demographic study (such as a cohort life table analysis) by replacing observations through time with the reconstruction of past environmental conditions. The cost for this compression of time is the effort required to collect the data needed to evaluate the many multivariate equations dictated by this technique.

Several assumptions are necessary to apply this demographic approach: (a) Birth rates and intrinsic survival rates ($\hat{S}_i$) are independent of time, (b) the state of each important environmental factor (e_j) can be determined for past conditions, (c) maximum favorableness (max e_j) can be determined independently, (d) the way environmental favorableness affects survival is adequately described by power-function relationships, and (e) the effects of environmental factors on survival are independent of one another. On the other hand, common assumptions of other techniques—such as stationary populations and homogeneous and constant environments—are not required in the analysis presented here.

Other limitations are also intrinsic to this approach. The method cannot address those environmental factors that leave no evidence except their effects on the population. Therefore, successful application will be limited by how well past environmental conditions can be reconstructed. There is no requirement, however, that the entire maximum life span of a population be analyzed. For example, if stand reconstruction can be accomplished only for the past 50 years, this method can still be applied to all individuals of a population less than 50 years old, even though some individuals in the populations might be much older. Such a study would produce estimates of potential survival and environmental constraints on survival over the first 50 years of the species's lifetime. Another limitation is that the independent variables in the final model might, in fact, be related. For example, the hypothetical case in Table 1 considers basal area and moisture index as independent variables. In most ecosystems, water availability will be determined, in part, by the amount of light reaching the understory, which would vary with stand basal area. Such statistical collinearity among the independent variables makes it difficult to interpret the estimated values of the parameters. In practice, however, the magnitude of β_{ij} might not be as important as whether $\beta > 0$ (showing that the factor had a statistically significant effect on survival) or $\beta = 0$ (the factor was irrelevant).

This model is based necessarily on plant age, which allows the description of plant development and environmental conditions with respect to the same temporal scale. Under many circumstances, however, birth and death rates are also strongly linked to organism size (Werner and Caswell 1977, Hughes and Connell 1987). The ability of the model to reveal demographic patterns will be less if size effects outweigh age effects.

Temperate-zone forest tree populations provide special advantages for the application of this demographic approach. Most temperate-zone trees can be aged easily by counting annual growth rings or annual bud scale scars. In addition, stand reconstruction techniques have been best developed in forests. Canopy gaps can be reconstructed from the presence of dead trees and tree fall mounds (Oliver and Stephens 1977) and the growth release date in neighboring trees (Henry and Swan 1974). Local climatic fluctuations (e.g., in temperature and precipitation) can be inferred from dendrochronological evidence (e.g., Graumlich and Brubaker 1986). Fire scars provide evidence of fire history (Barrett and Arno 1988). Historical records chronicle past hurricanes and other severe storms (Oliver and Stephens 1977), fires, and major insect outbreaks. Independent chronosequence or permanent plot studies (Alaback 1982, Agee and Huff 1987) can provide estimates of the past state of less detectable environmental factors, such as the cover of competing herbaceous species. Other factors are

more difficult to reconstruct because they do not supply enough evidence of their occurrence. For example, the influence on population dynamics of disease or minor or chronic herbivory would be difficult to assess using the demographic analysis described here.

Few methods have been available for estimating demographic parameters of long-lived species, such as Pacific Northwest trees. If stand reconstruction techniques can supply accurate descriptions of past environments, then the demographic analysis described here should be a useful tool for understanding the population dynamics of long-lived trees. In addition, discovered patterns of survival and environmental constraint can suggest further study. In particular, this type of demographic analysis can suggest specific hypotheses (that can be tested experimentally) about environmental control of population dynamics.

Acknowledgements

James S. Clark, Everett M. Hansen, Joseph E. Means, Anne W. Smith, and anonymous reviewers provided helpful comments on the manuscript. This work was partially supported by NSF grants DEB-80-12162 and BSR-85-14325.

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Appendix

Nonlinear multiple regression of the N_x against the F_j in equation 7b produces estimates of the parameters $N_0 \cdot \hat{S}_1, \hat{S}_2, \ldots, \hat{S}_3$, and the β_{ij}s. This estimation procedure is equivalent to analyzing a series of simultaneous equations. The data from Table 1 for tree densities within three age classes and six environmental sequences corresponds to a series of 18 simultaneous equations. These equations are best represented in matrix form. Let Y be the dependent variables, the N_x values. Then, for the hypothetical data in Table 1:

$$Y = \begin{bmatrix} 261.7 \\ 60.6 \\ 27.3 \\ 214.8 \\ 59.5 \\ 27.1 \\ 161.5 \\ 10.1 \\ 7.7 \\ 96.2 \\ 3.9 \\ 1.1 \\ 191.1 \\ 31.7 \\ 18.1 \\ 105.2 \\ 8.5 \\ 1.6 \end{bmatrix}$$

Let X be the matrix of independent variables. X consists of both indicator variables, indicating the inclusion or exclusion in the model of the parameters $\hat{S}_2$ and $\hat{S}_3$, and quantitative variables, the F_j. For the data in Table 1:

$$X = \begin{bmatrix} 0 & 0 & 0.5 & 0.7 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0.6 & 1 & 0.5 & 0.7 & 1 & 1 \\ 1 & 1 & 1 & 0.6 & 0.6 & 1 & 0.5 & 0.7 \\ 0 & 0 & 0.6 & 0.6 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0.8 & 0.8 & 0.6 & 0.6 & 1 & 1 \\ 1 & 1 & 0.8 & 0.5 & 0.8 & 0.8 & 0.6 & 0.6 \\ 0 & 0 & 0.2 & 0.6 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0.5 & 0.8 & 0.2 & 0.6 & 1 & 1 \\ 1 & 1 & 0.8 & 0.5 & 0.5 & 0.8 & 0.2 & 0.6 \\ 0 & 0 & 0.2 & 0.4 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0.4 & 0.5 & 0.2 & 0.4 & 1 & 1 \\ 1 & 1 & 0.2 & 0.3 & 0.4 & 0.5 & 0.2 & 0.4 \\ 0 & 0 & 0.4 & 0.6 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0.7 & 0.8 & 0.4 & 0.6 & 1 & 1 \\ 1 & 1 & 0.8 & 0.5 & 0.7 & 0.8 & 0.4 & 0.6 \\ 0 & 0 & 0.3 & 0.4 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0.3 & 0.6 & 0.3 & 0.4 & 1 & 1 \\ 1 & 1 & 0.3 & 0.4 & 0.3 & 0.6 & 0.3 & 0.4 \end{bmatrix}$$

For example, the second rows of X and Y correspond to the single equation

$$60.6 = N_0 \cdot \hat{S}_1 \cdot \hat{S}_2^{1} \cdot \hat{S}_3^{0} \cdot 0.6^{\beta_{11}} \cdot 1.0^{\beta_{12}} \cdot 0.5^{\beta_{21}} \cdot 0.7^{\beta_{22}}$$

where the values of N_x and F_j come from the first environmental sequence in Table 1.

The hypothetical data discussed in the text (Table 1) were analyzed using the Marquardt iterative method of nonlinear multiple regression (using Statgraphics, STSC Inc.). This technique requires initial estimates of the parameter values. A convenient way to derive these estimates is to transform logarithmically both sides of equation 7b:

$$\log N_x(t) = \left\{ \log N_0(t\text{-}x) + \sum_{i=1}^{x} \log \hat{S}_i \right\} + \left\{ \sum_{i=1}^{x} \sum_{j=1}^{v} \beta_{ij} \cdot \log F_j(t\text{-}x+1) \right\}. \quad \text{(A1)}$$

Equation A1 has the form

$$Y = A + B \cdot X.$$

The series of log-transformed equations A1 can then be solved by multiple linear regression. Although the estimates of the β values will be statistically biased, they are good starting points for the unbiased estimation procedure of iterative, nonlinear multiple regression.

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Movements, Habitat Use, and Spawning Strategies of Arctic Grayling in a Subalpine Lake Tributary[3]

Abstract

Spawning Arctic grayling *Thymallus arcticus* were uniquely marked in Upper Granite Lake, Washington to determine the movements, habitat utilization patterns, and reproductive strategies employed by individual fish. Prespawning behavior began in the shallows in the vicinity of the inlet stream as the lake became ice-free and spawning in the inlet stream persisted for approximately three weeks. Subdominant males held in refuge areas or actively cruised through the spawning grounds in search of mating opportunities. Dominant males were significantly larger, established territories, and enjoyed higher reproductive success than nonterritorial males. Dominant males were generally subdominant for periods before and after their territorial phase. Fifty-seven percent of the males defended territories at some time during the season. Both sexes spawned with a variety of mates. The number of spawners and level of activity in the stream was low in the morning and high in the midafternoon and evening. The distribution of spawners shifted downstream concurrently with a reduction in stream level; they were not observed in shallow riffles or in stream velocities above 0.21 m/s. Proximity of refuge areas to male territories helped maintain a substantial number of females on the spawning grounds. The number of visually isolated breeding territories and refuges in feeder streams was controlled by the aggressive behavior of males which in turn limited the production of this population.

Introduction

Gamefish management agencies have considered or have already introduced Arctic grayling *Thymallus arcticus,* into high elevation lakes of states in the Rocky Mountain and western region of the United States (Hubert *et al.* 1985). Establishment of self-sustaining populations in these remote areas is more desirable than maintaining populations through regular hatchery planting programs. Consequently, knowledge of the spawning behavior and the environmental requirements of spawners and incubating eggs are needed to successfully establish naturally reproducing populations.

Previous works on spawning behavior of Arctic grayling, *Thymallus arcticus* (Brown 1938, Kruse 1959, Bishop 1971), and European grayling *Thymallus thymallus* (Fabricius and Gustafson 1955), contained general descriptions of temporal patterns of stream use by the spawners. These authors reported that spawning begins at the time of ice breakup and lasts three to four weeks during which males established territories around midday, and spawning occurred from midday until after dusk. Spawners generally retreated to the lake or a quiet pool after dark, then reoccupied the spawning ground near midday the following day. When space was limiting, only dominant males established territories (Fabricius and Gustafson 1955), and due to the aggressiveness of territorial males, females and subdominant males tended to congregate outside the perimeter of dominant males' territories.

I describe temporal habitat-use patterns of mature Arctic grayling during the 1981 spawning season in Upper Granite Lake, Washington. This population descended from Montana stocks introduced in 1947. This is presently the only naturally reproducing population in Washington, so knowledge of habitat utilization and potential limitations to reproduction are essential for enhancement here and for evaluation of a potentially expanded management program for Arctic grayling in the state. By recording movements of individual fish, I detected previously unreported aspects of Arctic grayling spawning behavior at the level of the individual including: residence times, habitat utilization, movements, and territory density in the stream.

Description of the Study Site

The 58 ha Upper Granite Lake (Figure 1), 14 km southeast of Marblemount, Skagit County, Washington lies in a remote basin of glacial origin at 1372 m elevation with depths exceeding 70 m throughout most of the lake.

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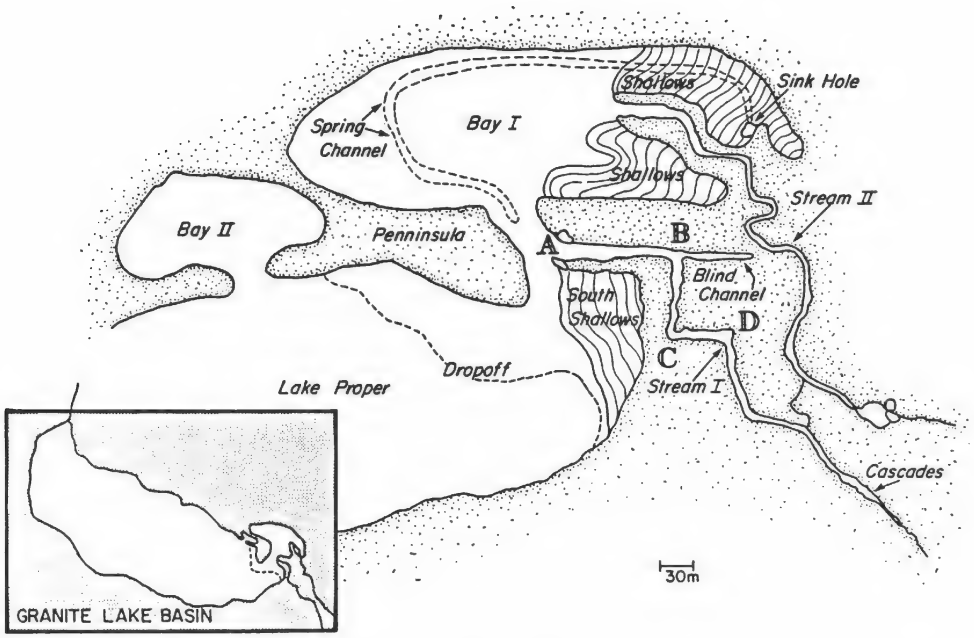

Figure 1. Map of Upper Granite Lake and the locations at the inlet end of the basin that were occupied by Arctic grayling spawners during the spawning season.

Two nameless inlet streams (here termed streams I and II) meander 400 m through a meadow at the east end of the lake. Stream I is a shallow riffle (mean depth = 25 cm) above point D and a glide (mean depth = 35 cm) below (Figure 1). The stream was primarily supplied by snowmelt, so flow varied considerably during the spawning season depending on temperature and the remaining snowpack (Table 1).

Arctic grayling only spawned in the lower 195 m of stream I, a series of three reaches separated by sharp bends between the mouth and Bend D (Figure 2). During high spring runoff, the lake level rose enough to back up the stream to site E (Figure 2) before surface flow became perceptible. An undercut at site B was 1.3 m deep along the outside bank. The rest of the stream bottom was uniformly flat, and was composed of several small sandy patches within a homogeneous mixture of sand and gravel (diameter < 8 cm). Patches of willow (*Salix* sp.) branches overhung or draped into the stream at irregular intervals below point D.

Stream II was not used by Arctic grayling. The stream gradient was such that a layer of silt and fine organic matter, sufficient to suffocate any incubating eggs, was deposited over the gravel during spring runoff.

TABLE 1. Water velocity measurements (m/s) in a tributary of Upper Granite lake in which grayling spawned in 1981.

Stream reach	28 June	9 July	10 July	16 July	20 July
Lower (A-B)	0.16	0.17	—	—	0.23
Middle (B-C)	0.18	0.13	0.12	—	0.32
Upper (C-D)	0.21	—	0.30	—	0.40
above D	>0.30	>0.30	>0.30	0.77	0.74

[1]See Figure 2 for location of the stream reaches.

Materials and Methods

Adult grayling were captured in fyke nets set in bay II or just off the mouth of stream I (Figure 1) and each fish was marked with individual color codes with two colored, celluloid, split, bird

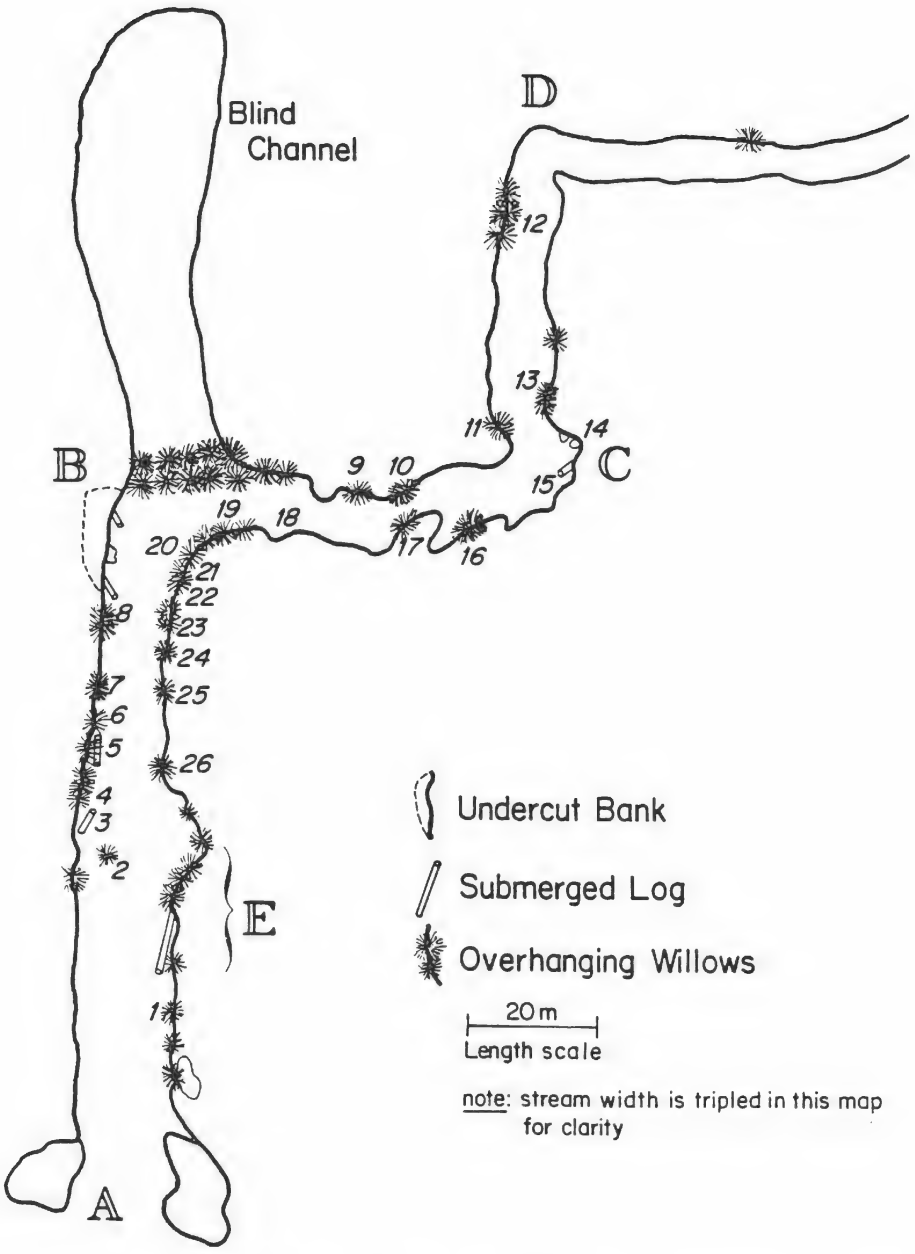

Figure 2. Map of the inlet stream to Upper Granite Lake. The numbered locations represent territories that were defended by male Arctic grayling on at least one day during the 1981 spawning season. Areas B and E signify the locations of refuges for females and subdominant males. A, B, C, and D indicate the mouth of the stream, and the first, second, and third bends in the stream.

rings attached to the leading edge of the dorsal fin (Bellamy 1980). The lower lobe of the caudal fin was punched with a paper punch to help monitor tag loss. The spawning population in 1981 was very small (53 ± 19 males and 39 (32 to 64 females); Beauchamp 1982) of which 75 percent, 35 males and 32 females, were marked for individual identification and observed over the duration of the spawning season.

No mortality from tagging was evident, but about 15 percent of the fish lost one or both rings during the first month. Fish that had lost one ring could still be identified visually by using one or a combination of characters such as sex, relative size, and color of the remaining tag. Tagging did not significantly affect the males' ability to hold territories ($X^2 = 2.49$, 1 *df*, $0.10 < P < 0.25$) nor to spawn successfully ($X^2 = 2.2$, 1 *df*, $0.10 < P < 0.25$).

Binoculars were used for identifying fish in Stream I and in areas of the lake above the dropoff. Males were easily distinguished from females primarily by their long irridescent blue dorsal fin and secondarily by the dusky body coloration of the males at peak maturity. Morning, midday, and evening observations were made daily at bay II, the spring channel, stream I, and the sink hole from June 26 to July 23. The outlet and lake proper were checked irregularly. I spent at least 5 min at each site observing the behavior and identity of the fish present. I studied each occupied area in the spawning stream for an additional 5 min to record the behavior of the resident males and to determine if the occupying male was territorial. Territory size was estimated visually from movements of the males in relation to prominent features at known distances apart within the stream.

Stream and lake temperatures were measured at 0.3 m below the surface during each observation period. Stream velocities were measured by timing a small semi-buoyant ball over a 7 m to 10 m distance in each of the stream reaches.

Results

Timing of the Spawning Season

Ice-out and the beginning of spawning ranged from mid June to early August between 1980 and 1985 with the duration of the spawning season averaging three weeks each year. Spawning Arctic grayling were observed in the stream from June 28 to July 20 in 1981. Numbers in the stream peaked during July 8-12 (Table 2). Mature Arctic grayling formed their first visible aggregation (10 to 20 fish) on June 27 off the mouth of bay II when the lake was only 40 percent ice-free. During the final stages of ice breakup (June 28), a few adult grayling entered the shallow waters of the study site and occasionally exhibited fragmentary courtship and agonistic behavior.

Pre-spawning Behavior Outside the Spawning Grounds

The majority of the early migrant adult Arctic grayling first appeared in bay II or the spring channel on 28 June, one day before the lake became ice-free. The fish presumably first aggregated here because these were the first sources of relatively warm water encountered by spawners migrating from under the ice toward the spawning stream. Arctic grayling showed only limited activity during their first day in shallow water. Males either paired with or aggregated around any females in these areas. Most females were not ripe early in the season and generally ignored the males' advances or threatened the males by erecting their dorsal fin (termed a dorsal display). Except for brief and infrequent spurts of activity these fish remained inactive for most of the day.

The lake became entirely ice-free on 29 June, and 15 adult grayling occupied bay II. These fish were extremely active during mid-afternoon. Numerous courtship displays, challenges, and abortive spawning attempts were observed. One male exhibited territorial behavior around a small patch of gravel in the bay. He attracted a female who entered the territory and assumed a submissive posture (depressed dorsal fin and caudal region, with the body resting on the substrate). When a second male attempted to court the female, the original male interrupted courtship to threaten the intruder. Both males circled the female while threatening each other with dorsal displays (the dorsal and pelvic fins erected in a non-directional manner). When their actions forced the female from her position, she circled inside the competing males in an apparent attempt to maintain her original position. The female maintained position and the submissive posture while the two males continued to interact within 2 m of her. Whenever other intruding

TABLE 2. The daily counts of adult Arctic grayling in each stream reach and refuge in stream I in 1981.

Date	Total number of spawners in stream	Stream reach from A to B	Refuge E	Refuge B	Stream reach from B to C	Stream reach from C to D
June 28	1	0	0	1	0	0
29	2	0	0	1	1	0
30	8	0	0	4	4	0
July 1	15	4	0	1	9	2
2	48	15	0	3	21	9
3	26	7	0	1	16	2
4	31	13	0	8	9	1
5	46	12	0	16	15	3
6	32	9	0	16	6	1
7	37	13	0	23	1	0
8	64	28	0	7	27	2
9	55	20	0	34	1	0
10	49	8	26	15	0	0
11	53	17	20	10	6	0
12	61	15	6	15	22	3
13	20	8	3	7	2	0
14	43	20	8	8	7	0
15	29	22	2	1	4	0
16	42	18	10	5	6	3
17	21	13	7	0	0	1
18	6	2	4	0	0	0
19	3	1	2	0	0	0
20	5	2	3	0	0	0
21	0	0	0	0	0	0
22	0	0	0	0	0	0
23	0	0	0	0	0	0

males approached, she either threatened with a dorsal display or ignored the intruder's advances. However, when the primary male returned, she reassumed the submissive posture and courtship proceeded.

The spawning attempts in the bay contained most of the components of a typical spawning sequence, but release of eggs and milt were not observed. The female's caudal region was often suspended above the substrate and gaping was absent during these false matings, whereas in real spawning events the tail was depressed and partially buried in the substrate. Normally, a courtship sequence would be interrupted numerous times by nearby males. Intense competition for females between the territorial male and intruding males was also observed by Fabricius and Gustafson (1955) for European grayling *Thymallus thymallus*.

Sexual Differences in Movement and Occupation Patterns by Spawners

The first male grayling arrived at the inlet stream 2 d before the first females. Males were always more numerous than females on the spawning grounds (sex ratio of 1.5:1.0 for the season). Males composed 51 to 59 percent of the stream population at the peak of the breeding period and nearly 100 percent at the beginning and end of the season.

The stream was partitioned into territories and refuge areas by the spawners. Dominant males established territories on the spawning grounds. For this study, a territory was defined as the area consistently occupied and defended by a dominant male. Most of the territories in stream I were located along the bank under a canopy of low overhanging willow branches. Even bare, single willow branches provided adequate

attraction for a territorial male despite the lack of cover. The stream bottom was comprised of an even mix of sand and gravel up to 8 cm in diameter. A territorial male normally stationed himself 10 to 20 cm from the edge of the stream under one of the middle branches of the willow canopy. Willow branches or some topographical feature of the streambed appeared to serve as reference points (territorial foci) within a territory around which a male oriented. The territories were generally delineated up and downstream by some other structure such as partially buried logs, stream bank irregularities, or the termination of a large willow canopy. Willow branches in many of the territories were submerged and restricted the view of upstream and downstream, but did not obscure vision laterally across the streambed. Other territories were associated with irregularities in the stream bottom or banks, as in territories 3, 18, 19, 24, and 25 (Figure 2). The stream was fairly even-bottomed and 3 to 4 m wide. As a result, a territorial male usually commanded the width of the stream over the length of his territory. The average size of a territory was 1.4 m^2 (SD = 1.2 m^2). Territories were generally rectangular with the short axis oriented along the direction of water flow with the width extending either across to the opposite bank or to some visual obstruction. The spawning area occupied by Arctic grayling in Stream I encompassed 663 m^2 with a mean stream width of 3.4 m and length of 195 m. This section stretched from 10 m below site 1 to about 0.5 m upstream of location 12 (Figure 2). Although the stream contained 26 territories that were occupied at some point during the spawning season (Figure 2), a maximum of only 14 were defended successfully at any one time.

Refuge areas afforded nonterritorial fish easy access to favorable spawning areas, while providing a sanctuary from the aggression of more active males. The refuge areas were located downstream from major spawning reaches in the stream. Refuges had negligible stream velocities due to internal eddies and submerged branches. Submerged willow branches and a deep undercut bank at site B, and submerged willow branches at site E (Figure 2) provided fish in the refuges with partial visual obstruction from aggressive males. Fish in the refuge areas were usually inactive, even when as many as 40 fish clustered together. While in the stream, subdominant males and females either remained in refuges or cruised up and downstream.

Temporal Occupation Patterns by Spawners in the Stream

The middle reach of the stream (from the refuge at B upstream to C; Figure 2) harbored 62 percent of the spawners from the beginning of the spawning season (June 28) until July 5 (Table 2). Before July 10, 65 percent of the observed spawning activity occurred in this section (Table 3). Grayling were relatively inactive on July 9 and 10 and congregated in refuge areas where there were overhanging banks and overhanging willows at sites B and E for cover.

TABLE 3. Number and location of spawning acts by Arctic grayling observed in stream I. (See Figure 1 for locations)

Date (July)	A-B Lower	B-C Middle	C-D Upper	Stream Level
1-8	3	15	4	High
9-10	1	0	0	Dropping
11-17	12	3	0	Low

Only station B (Figure 2) was used as a refuge area from June 28 to July 9. Stations B and E were used from July 10 to 16, and only station E for the rest of the spawning season (Table 2). As the lake waters receded after July 9, the stream level dropped an average of 11 cm by July 10. The reduced depth resulted in a slight change in stream velocity in the middle reach (from 0.18 to 0.12 m/s), but significantly altered the upper reach with increased velocity (from 0.21 m/s to $\geq$ 0.30 m/s) and reduced depths to only 3 to 8 cm (Table 1). Concurrent with changes in flow, 82 percent of the spawners shifted to the lower reach of the stream (including refuges B and E) after July 9 (Table 2).

Arctic grayling showed net movement into the spawning stream during the day and out to the lake at night. On average, 30 grayling visited the spawning grounds per day, with 25 spawners in the stream at dusk, but only 15 present in the morning. The diel occupation pattern was most pronounced during the first week of the season: an average of 5 grayling (60 to 100 percent males) remained overnight through midafternoon when 30 additional spawners moved into the stream. The difference between day and night occupation levels decreased as the season progressed. More spawners entered the stream during the

day (mean: 8.6 males, 7.2 females) than at night (mean: 1.9 males, 1.5 females), whereas more spawners left the stream at night (mean: 7.0 males, 6.0 females) than during the day (mean: 3.4 males, 2.5 females).

Most of the fish that remained in the stream overnight gathered in refuge areas. Of the males that stayed overnight, 25 percent continued to occupy the locations that had been their territories during mid afternoon and early evening but no longer defended them. Males and females occupied these sites together until midday, when activity increased and dominant males again began to express territoriality. The female and subdominant males then either moved to the main refuge areas, left the stream, or began to "cruise" the spawning grounds. A higher percentage of females than males remained in refuges during the day (Table 4). Spawners that had migrated to the lake the previous night and new arrivals generally entered the spawning grounds from late morning through afternoon (Table 4). As the afternoon progressed, slightly fewer fish remained in refuge areas as more males established territories and other males and females began cruising among territories and refuges.

By monitoring the movements of individually identifiable males, I determined the turnover rate of occupants in the refuge areas each day. As some of the males that had remained overnight ("veteran males") left the refuge areas, they were replaced by new arrivals from the lake. On the average, 55 percent of the veteran males left the refuges near midday and either (1) established territories (17 percent), (2) cruised the stream (23 percent), or (3) left the spawning grounds (15 percent). Of the newly arriving males, 44 percent occupied refuges and 47 percent began cruising. Only one new arrival established control of a territory during his first day in the stream.

Fish that remained in the Spring Channel most of the day often moved into the stream during the period of greatest daily activity (1500 to 2100 hours). Arctic grayling that migrated from the stream one day did not necessarily return on the following day.

Behavior on the Spawning Grounds

During 30 June and 1 July the number of adult Arctic grayling utilizing bay II diminished while numbers entering stream I increased. Females first entered the stream on June 30, 2 days after the first males appeared. Mild courtship behavior and very little territorial behavior was evident on that day. The first spawning event was observed on 1 July at station 19 and involved an unmarked female and the territorial male.

The spawning season in 1981 lasted 23 days from 29 June to 20 July. Spawning activity commenced the day of ice out with many mature fish moving into shallower regions of the lake. Males preceded females to the spawning grounds by 2 days. Males were numerically dominant within the stream at the beginning of the day, but the male to female ratio normally decreased as the day progressed. Male spawners were larger (mean fork length of 387 mm) than the female spawners (mean fork length of 364 mm). The size composition of the stream occupants did not change during the spawning season, and was not a factor in the time of arrival or departure by either sex. For the first 4 days of the spawning season, half of the spawning acts observed involved the same male while the remaining spawning acts were spread evenly among five other males (Table 5).

A territorial male normally challenged any male intruder, but fish travelling along the margin of the stream opposite a male's station were less likely to be attacked. Territorial males used a hierarchy of threat displays and actions. From least to most intense these included: a simple dorsal display, a lateral dorsal display, a mutual lateral dorsal display, lateral shoving, nipping, and chasing. The lateral dorsal display was a simple dorsal display performed alongside the intruder. If the intruding male persisted, the

TABLE 4. Daily occupation pattern of veteran males, newly arriving males, and females on the spawning grounds (seasonal averages of daily counts).

	Refuge	Territorial	Cruising	Total
Veteran Males				
Morning	5.7	1.9	0.1	7.7
Midday-evening	2.4	2.9	1.4	6.7
Newly Arriving Males				
Morning	0.1	0.0	0.1	0.2
Midday-evening	2.2	0.5	0.4	3.1
Females				
Morning	5.3	—	1.3	6.6
Midday-evening	5.6	—	4.8	10.4

TABLE 5. Observed spawning acts recorded by location, male strategy and the mark codes of the female and male spawners observed: nm = no mark, lost = lost tag, nm* = different unmarked fish, pl = purple, o = orange, b = blue, y = yellow, r = red, g = green, w = white, TMI and TMII= Territorial Male I and Territorial Male II, the early unmarked, but identifiable territorial males.

Female	Male	Male Strategy	Spawning Location[1]	Date	Time
nm	TMI	territorial	19	July 1	1750
plpl	pbw	cruising	above 11	2	1515
nm*	TMII	territorial	20	2	1555
nm*	TMI	territorial	19	2	1600
pl-	TMI	territorial	19	2	1605
nm	TMI	territorial	19	2	1615
plpl	TMI	territorial	19	3	1755
nm	pgw	cruising	above 19	4	1450
ob	plgy	territorial	8	4	1550
oo	nm	territorial	12	4	1550
oo	nm	territorial	23	5	1740
nm	nm	territorial	9	8	1500
nm	pgw	transient terr.	9	8	1500
-y	rp	territorial	9-17	8	1505
ry	nm	territorial	16	8	1510
ry	ply	territorial	15	8	1515
ry	nm	territorial	14	8	1520
plgb	nm	territorial	14	8	1520
nm	nm	territorial	9	8	1620
ry	nm	cruising	9-17	8	1820
ry	nm	territorial	9	8	1830
w-	nm	territorial	9	8	1830
nm	ply	territorial	23	9	2030
nm	ply	cruising	B	11	1730
ogw	ply	territorial	20	12	1420
ogw	ply	territorial	20	12	1421
ogw	nm*	territorial	19	12	1425
ww	nm*	cruising	8	13	1730
ogw	lost	cruising	13	13	1745
ogw	pgo	cruising	between B&E	14	1750
ogw	plr	cruising	between B&E	14	1750
ww	opl	territorial	23	14	1840
rr	nm	territorial	19	14	1845
by	go	territorial	above 26	14	1630
ogw	nm	territorial	17	15	1638
ogw	go	territorial	8	15	1643
yy	nm	cruising	B	16	1450
ogw	go	cruising	5-6	17	1500

[1]The location codes are shown on Figure 1.

territorial male continued to display while attempting to shove the intruder off the territory. If this maneuver was unsuccessful, either of the males might circle around the opponent and nip at the tail, caudal peduncle, or the posterior base of the dorsal fin. The confrontation usually ended with the loser (generally the intruder) being chased from the territory. When spawning and courtship activity was high, the chase usually terminated at the edge of the territory. However, when fewer fish were present and spawning activity was low, the winner often chased the loser the length of the spawning area. Males patrolled the length of their territories, and frequently intruded on a neighboring territory to challenge that male or test the boundaries of the territory. Dominant males occasionally left their territories and briefly cruised the spawning grounds before returning to reestablish control of their territory. Much of the activity in the afternoon and evening consisted of territorial males threatening and chasing cruising males that passed their territories.

At the beginning of the spawning season, male grayling in bay II and in stream I exhibited more male to male aggression than male to female courtship. During the first week of the spawning season, males readily interrupted courtship to attack other males that ventured too close (within 1 to 2 m). As the season progressed, the courting male positioned himself between the female and the intruding male, but continued spawning with the female rather than confront the intruder.

Thirty-seven complete spawning acts were witnessed during the course of the season, and a generalized description of the spawning sequence emerged from these observations. A territorial male generally courted any female in or near his territory. A male would move alongside or slightly ahead of the female, extend his dorsal fin and tilt his body roughly 60° toward the female, and then drift toward the female while slightly vibrating his entire body. If the female was not ready to spawn she hurried past the territory. Males often followed for quite a distance attempting further courtship. If the female was receptive she remained in place and assumed the submissive posture. The male continued to quiver and move alongside the female to cover her back with his fully extended dorsal fin. Fabricius and Gustafson (1955) hypothesized that the male dorsal fin acted as a clasping organ. The male's mouth gaped as they quivered, and after a couple of seconds the female also began to quiver and gape slightly. At this point the male placed his caudal peduncle across the female's, and rotated his tail parallel to the stream bed. As the spawners' quivering increased in frequency and amplitude, the female bent her caudal peduncle downward with the tail up, thus forcing her vent into the substrate. The spawners' quivering motion forced the female's vent further into the substrate until her caudal peduncle was almost buried. These actions swept the accumulated fine sand and silt from around the nest site and created a transient depression for egg deposition. The spawners' mouths gaped wider as eggs and milt were released. Spawning acts normally lasted 14 s with a range of 9 s to 25 s. Males normally returned to their station following the spawning act, whereas females normally rested near the nest for several minutes before leaving the territory or returning to spawn with the same male again.

Arctic grayling spawn promiscuously. Although no count was attempted of the number of times specific males and females spawned, random observations of spawning activity included: (1) a male spawning five times in 3 d with at least three different females (including three times within 15 min), (2) a male spawning three times with two different females over three d and spawning twice in 5 min, (3) a male spawning five times over 4 d with three different females and spawning twice within 1 min, (4) a female spawning nine times with seven different males in 6 d and three times in 5 min, (5) a female spawning five times within 3.3 h with at least four different males (Table 5).

Female Arctic grayling appeared to select both her mate and the precise location of the spawning site. As in bay II, if courtship with a territorial male was interrupted by male intruders, the female remained over the same site in her submissive posture while the dominant male defended his territory. If one of the intruders attempted to court her, she darted off temporarily, but returned to the same site within seconds. Spawning normally occurred only with the territorial male in these situations.

While on the spawning grounds, females normally remained in a refuge area or actively sought mates. As females ripened, they tended to cruise more actively. Normally, males

intercepted and attempted to court the passing females. Upon encountering a courting male, the female often moved to some other site within the territory while the male was quivering alongside her. The pair then completed the spawning act in this new location. When a female entered a male's territory and assumed the submissive posture, spawning would proceed. However, if the male's advances moved the female from the site where she had assumed the submissive posture, she terminated the spawning attempt and either left the territory, moved to another location within the territory, or circled back to the original site. If the female remained inside the territory after the interrupted atttempt, spawning proceeded. In either case the female appeared to select the specific site for depositing her eggs. How the female evaluated a nest site could not be ascertained from my field observations.

Fifty-seven percent of the male spawners exhibited territorial behavior. The average territorial male preceded his territorial phase by cruising for 2.5 (SE = 0.5) d. These males held territories an average of 4.1 (SE = 0.5) d followed by another 1.5 (SE = 0.3) d of cruising. Thus territorial males returned to or remained on the spawning grounds significantly longer (8.1 d; SE = 1.3 d) than females and subdominant males (two-sample T-test, $P < 0.005$). Kruse (1959) reported that male grayling in Grebe Lake, Wyoming, defended territories for 4 to 7 d and females remained from 1 to 3 d. The number of days a male cruised the stream prior to becoming territorial was not related to the number of days he was territorial ($r = 0.097$, 18 *df*). However, the number of days a male cruised the stream after being territorial was inversely related to the duration of territoriality ($r = -0.482$, 18 *df*, $P < 0.05$).

Territorial males were significantly larger (mean fork length = 395.3 mm, SE = 3.3 mm) than subdominant males (mean fork length = 377.7 mm, SE S= 5.6 mm; two sample T-test, $P < .025$), and larger males held territories longer than smaller males ($r = 0.578$, 10 *df*, $P < 0.05$). The size of males was not correlated with total residence time in the stream ($r = 0.268$, 23 *df*, $P > 0.10$). Although both territorial and cruising males spawned successfully, territorial males were 2.1 times more successful than cruising males in acquiring matings ($X^2 = 50.2$, 1 *df*, $P < 0.005$). The ratio of cruising males to territorial males involved in observed spawning events changed from 3:19 between 1 July and 8 July to 7:9 from 9 July to 17 July ($X^2 = 12.3$, 1 *df*, $P < 0.005$). Cruising males spawned either in peripheral areas of marginal quality or inside a territory while the dominant male was either courting a different female, defending against other intruders, or challenging a neighboring male.

Discussion

Some characteristics of the behavior and movement of spawning Arctic grayling from Upper Granite Lake were similar to that of other populations. The duration and timing of the spawning period in relation to ice-off in Upper Granite Lake was similar to that reported for other populations (e.g., Kruse 1959, Peterman 1972, Kratt and Smith 1980). Bishop (1971) and Peterman (1972) observed diel movement in and out of the spawning stream similar to that reported here. Peterman (1972) concluded that this movement was closely related to water temperature. Kratt and Smith (1980) constructed an ethogram of the spawning behavior of Arctic grayling showing the relative frequencies of each event in the sequence of 55 spawning attempts. Their observations were very similar to mine except that they never observed females signaling readiness with a submissive posture.

The supply of potential territories was scarce in the tributaries to Upper Granite Lake. Only the larger, dominant males held territories. This was also observed by Kratt and Smith (1980) for a population spawning in the outlet of Black Lake in northern Saskatchewan, Canada, but the average sizes of the territories there and elsewhere were larger than in this study. Territorial males experienced higher reproductive success than subdominant males, which were unable to hold territories against frequent challenges by other males.

Early arrival on the spawning grounds would seem adaptive for increasing an individual male's fitness, since it would presumably be easier to acquire a vacant, favorable site with little effort when few competitors were present. Once in control of a territory, the male might enjoy a "home-court" advantage over challengers. I observed only one territorial male being displayed by another male. The advantages of early arrival

were balanced somewhat by the higher risk to the early zygotes of dislodgement by subsequent spawning activity. Since the spawning season lasted five times longer than the territorial tenure of individual males, the early-arriving males had no chance of protecting their offspring from disturbance by the later spawners. Furthermore, very few females were fully ripe at the beginning of the spawning season, so early territorial males had to either attract most of the early females (which they did), or hold their territories until more females ripened (this could not be adequately determined).

The switch in priorities from aggression to courtship by males probably resulted from a change in the degree of maturation of the spawners during the season. Another factor might be that the males were evaluating their opponents early in the season. Once the dominance hierarchy was established, potential competitors could probably predict the outcome of a challenge and thus avoid challenges that were clearly futile. Thus, the males could concentrate more on courtship and spawning than on aggression. Also, as the season progressed, more ripe females became available, and any unprovoked agonistic interaction with other males would detract from the time and energy that could be invested in acquiring more matings.

The males' transition from the cruising strategy to territoriality and back to cruising might relate to changes in maturity of individual males over time. Aggression normally increases with gonadal maturation and hormone production such that males achieve full competitive potential when fully mature. The degree of maturation of a new arrival to the spawning grounds would presumably be lower than that of males already present. New arrivals, consequently, might not be as aggressive as fully mature, but otherwise equal males. As a result, new arrivals would not compete as successfully for a territory. The only option available to subdominant males would be to cruise while maturation progressed. Males that were able to become territorial expressed this ability at peak maturity. Males lacking this potential remained subdominant and followed the cruising strategy. The hormone level in dominant males might decline after a period of territoriality and spawning, thus reducing aggressiveness and the ability to hold a territory. At this point, these males might either terminate spawning activity or revert to the cruising strategy. Males did not lose control of their territories (with one exception), but rather they simply did not attempt to defend a site the next day.

Many of the Arctic grayling that did not return to the stream on consecutive days were often sighted in the sink hole or the spring channel instead. A further benefit to partially spent males of leaving the stream would be to ripen their remaining gonadal material more rapidly in warmer water, thus expediting their return to the spawning grounds. The shallows (mean temperature 0.5 m below the surface was 10.0°C) and the lake proper (6.2°C) were considerably warmer than the stream (3.0°C) throughout the spawning season.

Females appeared to select the nest sites, but the cues used to select these sites could not be determined by field observation. Olfactory cues could be important. The female might visually assess the substrate and feel the stream velocity as she enters the territory; or she might probe the substrate with her fins while assuming the submissive posture. Since Arctic grayling eggs are only half the diameter of trout eggs, and are not buried in a redd, the important features of a spawning site might be related more to stability of the streambed (i.e., substrate size scaled appropriately to the range of stream velocities occurring during the incubation period) than to interstitial volume.

The pattern of spawner density shifted among stream reaches in response to changes in the quality of the available spawning habitat; the location of the preferred refuge changed concurrently. Refuges allowed the females and subdominant males to rest unmolested downstream from, but near the area of highest spawning activity and territorial occupation. A substantial number of spawners occupied the Spring Channel most of the day, entering the spawning grounds only during the period of highest activity (mid-afternoon to early evening). These fish would benefit from accelerated maturation of gametes in warmer water, easy accessibility to the spawning grounds, and refuge from instream aggression by territorial males.

Female spawners behaved much like cruising males. They left the stream more readily than territorial males. While in the stream, unless actively

spawning, they remained in a refuge area or cruised the stream.

Above the uppermost location of grayling spawning activity (point D, Figure 2), the stream was a shallow riffle (3 to 8 cm deep) with higher water velocities ($>$ 0.3 m/s) than in the lower reaches ($<$ 0.2 m/s). The reach above the bend at C also became a shallow riffle midway through the season with stream velocities exceeding 0.2 m/s. Spawners apparently avoided the riffle section in response to excess water velocity and insufficient depth. This population spawned exclusively in stream velocities lower than the range of velocities reported by Krueger (1981) for spawning Arctic grayling in Alaska. The adaptive significance of this avoidance became evident during the incubation period. The stream depth dropped below 1 cm above point D as runoff from snowmelt diminished. Eggs deposited in the faster flowing reaches would probably have either been dislodged by high velocities early in the season, dewatered later in the season, or subjected to lethally high temperatures before hatching. The highest densities of Arctic grayling in the Big Hole River drainage, Montana were found in reaches where the average stream velocity was 0.21 m/s during the summer, but spawning normally occurred in the smaller, and presumably slower-flowing, tributaries (Liknes and Gould 1987).

Some spawners occupied these riffles in 1985, but all were 3 year olds, the smallest, youngest spawners in the population. Three year olds were absent during the 1981 season, which resulted in a much smaller spawning population. Based on the observations in 1981, the absence of 3 year olds in 1981 might have resulted from high incubation mortality induced by the low snowpack and early runoff in 1978. Occupation of the riffle zone by only the youngest spawners suggests that these first time spawners were forced into these low quality areas by the larger, experienced males in the more favorable reaches downstream. Spawners that attempted courtship displays and spawning in the riffle area had difficulty maintaining position in the current.

In streams where habitat characteristics change frequently, the flow regime and availability of adequate territorial sites play an important role in determining the occupation pattern of the spawners over time. In high altitude lakes with short inlet watersheds, shifts in spawner occupancy would occur quickly in response to rapid changes in streamflow. If the spawners were condensed in response to the rapid contraction of adequate spawning habitat, poor reproductive success might result from either superimposed spawning or increased behavioral interference among the males. Fabricius and Gustafson (1955) hypothesized that the lack of refuges reduced spawning success because the females were literally driven off the spawning grounds by aggressive males.

Promiscuity offered several adaptive advantages to spawners in this population. Females could choose a variety of mates, and thus increase the diversity in the genome of their progeny. In a small population of spawners, this might lower the risk that most or all of a spawners' progeny would suffer from debilitating double recessive genes common with inbreeding. By spawning in a variety of territories, females distributed their eggs in a variety of microhabitats, thus minimizing the risk of losing all their progeny to localized impacts of overspawning, dewatering, disease, and predation. Males increased the genetic diversity of their progeny by attracting a variety of females to their territory. Dominant males that have reverted to cruising and subdominant males would also diversify the locations where their progeny incubate, because the probability of a cruising male spawning repeatedly in the same location would be low.

When evaluating lakes for potential introductions of Arctic grayling, two critical aspects of their spawning behavior need to be considered. First, the eggs are not buried and are vulnerable to high water velocities and streambed disturbances; and second, male aggression might inhibit spawning success when the streambed lacks visual isolation between dominant males. Feeder streams of low gradient with stable discharge are highly desirable, but rarely exist in drainages of high altitude lakes. Meandering meadow streams with abundant springwater inflow are more likely to provide the essential flow stability for reproduction of lake-dwelling Arctic grayling. The instream structural complexity of rocky or woody debris, vertical relief across the channel, and channel bends help increase the density of potential territories. Courtship activity always attracts the attention of cruising or neighboring territorial males. Thus potential spawning sites that are close to and in full view of territorial

males are not favorable because the presence and activity of another male would increase the rate of agonistic interaction. The aggressiveness of territorial males prevented occupation of potential spawning sites adjacent to territories. The scarcity of adequate territorial sites probably contributed to the high incidence of male cruising. Fabricius (1951) suggested for *Tanichthyes albonubes* and *Abramis brama* that an increase in production might be achieved by adding complexity to the streambed, thus visually partitioning the spawning grounds and allowing males to establish the maximum number of territories.

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Received 25 September 1989
Accepted for publication 14 February 1990

Acknowledgments

I thank Dr. Richard R. Whitney for his constant support, advice, and review of the manuscript; and Drs. Ernest L. Brannon, Gilbert B. Pauley, P. H. Eschmeyer, and Thomas E. Kruse for their reviews of the manuscript. The Washington Cooperative Fish and Wildlife Research Unit and the Washington State Department of Wildlife provided support for this study.

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Cambrian and Upper Devonian Carbonate Lithologies of the Whitefish-MacDonald Range, Northwest Montana and Southeast British Columbia, A Preliminary Report

Abstract

This study describes undifferentiated Cambrian and Upper Devonian carbonate rocks in the northern Whitefish Range of northwestern Montana and the contiguous MacDonald Range of southeastern British Columbia. An 804 m thick section on Inverted Ridge, British Columbia is described in this report.

Cambrian lithologies are dominated by bioturbated, dolomite and lime mudstones and are interpreted as having been deposited in a mostly subtidal marine environment. Upper Devonian lithologies contain bioturbated, dolomite and lime mudstones, algal and stromatoporoid dolomitic and lime bindstones and crinoid-intraclast, dolomitic and lime wackestones. The Devonian rocks are interpreted as having been deposited in a subtidal to intertidal, occasionally supratidal marine environment. The Cambrian-Devonian contact is placed at the base of a distinct sandstone unit characteristic of Devonian strata in the southern Canadian Cordillera.

Lithologic data obtained from this study will be useful in the continuing exploration for natural gas and oil in the Rocky Mountain Fold and Thrust belt. Paleoenvironmental interpretations will fill a large void on regional paleogeographic maps. Finally, conodont age dating of the Devonian rocks of this study has accurately placed their time of deposition as during the latest Frasnian to Middle Famennian ages of the Late Devonian Epoch.

Scope of Investigation

Thrust-faulted blocks of undifferentiated Cambrian and Upper Devonian carbonate rocks are exposed in the northern Whitefish Range, Lincoln and Flathead counties northwestern Montana and the contiguous MacDonald Range of southeastern British Columbia (Figure 1). In adjacent northwest and central Montana (Missoula-Philipsburg area), equivalent rocks include the Cambrian Hasmark Formation, the Jefferson Formation and the Devonian portion of the Three Forks Formation (Figure 2). Lower Paleozoic units defined by these lithologies have been mapped and stratigraphic sections measured (Price 1962; Norris and Price 1966; Mudge 1977, 1982; Whipple, pers. comm. 1988), but detailed sedimentologic and biostratigraphic data have not been published. The purpose of this article is to provide a detailed description of the previously undifferentiated carbonate rocks exposed in the Whitefish-MacDonald Range.

Location of the Study Area

The Whitefish-MacDonald Range is located within the Rocky Mountain fold-and-thrust belt in Lincoln and Flathead counties, northwestern Montana and southeastern British Columbia, respectively. The range is bounded on the north by a line parallel to and 24 km north of the International Boundary, on the south by Lat. 48 degrees, 30 minutes north, on the east by Glacier Park and the North Fork of the Flathead River, and on the west by the drainage between the Whitefish and Salish ranges. The section of rock measured in this study is located on Inverted Ridge in southwestern British Columbia, 24 km north of the International Boundary.

Methods of Study

Field work was conducted during July and August, 1987 and 1988, and October, 1989. The section was measured using a Jacob's staff, Brunton compass, and steel tape. Information gathered in the field included descriptions of lithology, bedding thickness, megafossil type, primary sedimentary features, and topographic expression. Oriented samples were collected at six meter intervals and at major lithologic changes. Samples were examined using acetate peels, polished slabs, and petrographic thin sections. Lithologic descriptions utilize the carbonate classification scheme of Dunham (1962), modified by Embry and Klovan (1971).

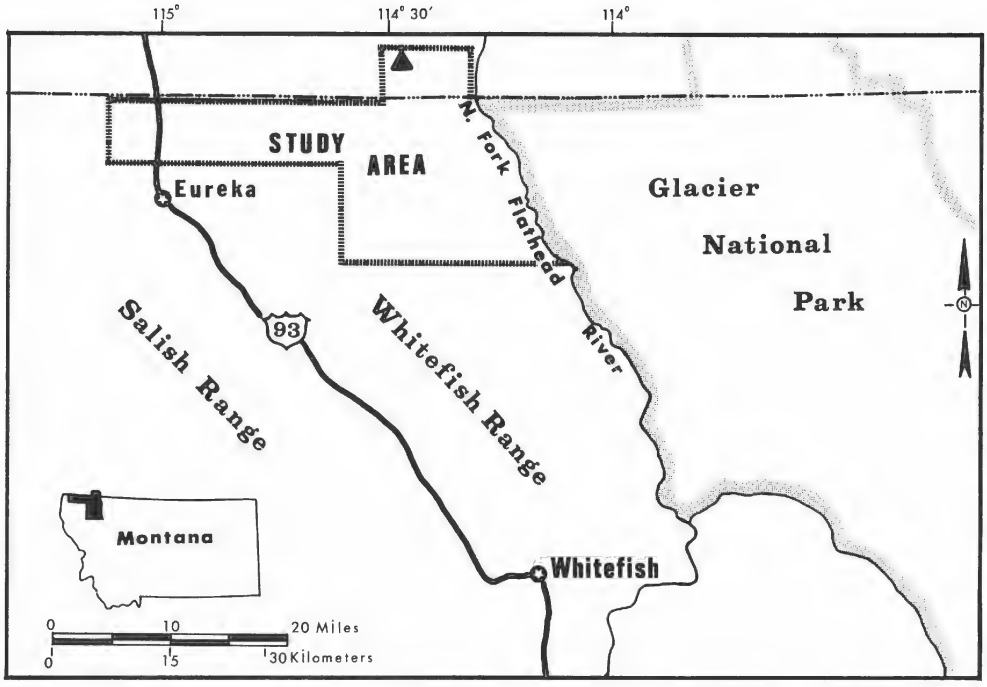


Figure 1. Location map of the study area. The position of the stratigraphic section at Inverted Ridge is indicated by the darkened triangle.

The Cambrian-Devonian Unconformity

In much of Montana Devonian rocks rest unconformably on Cambrian rocks. In southeastern British Columbia, at Inverted Ridge, Upper Cambrian, Ordovician, Silurian, and all but Upper Devonian rocks are missing. In this study the Cambrian-Devonian unconformity is placed at the base of the distinctive six-meter thick calcareous quartz arenite (Unit 2) 242 m above the base of the Cambrian carbonate interval. This interval is noted on Figure 3, the Inverted Ridge Graphic Section.

The base of the quartz arenite was chosen for several reasons. First, Late Devonian conodonts are present 70 m above the quartz arenite without a distinctive lithology change or unconformity observed between the sandstone and typical Devonian lithologies higher in the section. Second, several authors (Price 1962, Norris and Price 1966) have described a similar thin sandy unit at the Cambrian-Devonian boundary at adjacent sections in Canada.

Inverted Ridge Section, British Columbia

In the MacDonald Range, at Inverted Ridge, the Cambrian and Devonian carbonate section is recognized as a series of brown and gray steep slopes and cliffs. The base of the section conformably overlies the well exposed characteristic green shale and thin limestone interbeds of the Gordon Shale which, in turn, overly the Flathead Sandstone. The contact between the first carbonate unit and the underlying Gordon Shale is conformable over several meters. The boundary is placed where the thin limestone beds exceed 50 percent of the outcrop.

The 804 m thick measured section at Inverted Ridge is divided into 13 stratigraphic units based on lithology. Each unit is briefly described. The description is followed by an environmental interpretation. Sample positions and assigned lithologic units are numbered and indicated on both the written and graphic logs.

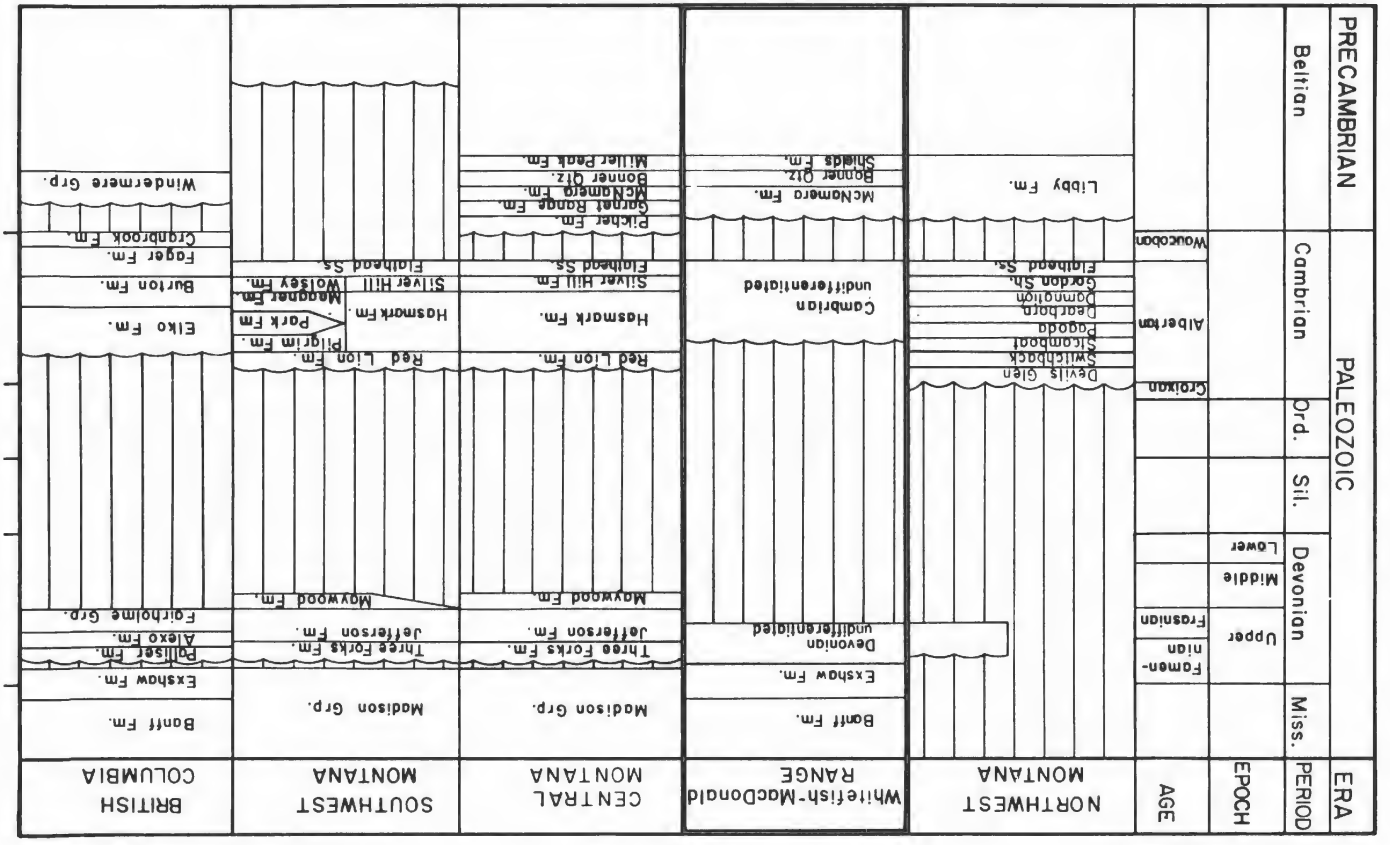


Figure 2. Regional stratigraphic correlation chart for Montana and southeastern British Columbia. The stratigraphic nomenclature for the Whitefish Range is highlighted by a thickened line (from Balster 1980).

Stratigraphic Sequence

Unit 1: Bioturbated Dolomite Mudstone (samples 1 to 26)

Description. The dominant lithology within the Cambrian interval of the Inverted Ridge section is a mottled, dolomitized mudstone that lacks preserved fauna. The unit is 221 m thick, mostly black on a fresh surface, and calcareous in the first 32 m. The unit is thin bedded with very thin shaly interbeds. Porosity is poor, vugs are few, and geopetal infilling of horizontal burrows is common. Fossils are absent except from the base to 22 m where disarticulated, abraded, unoriented trilobite and linguloid brachiopod fragments are common. At 170 m and 190 m above the base cryptalgal laminations are present.

Environmental Interpretation. The mottled mudstone indicates infaunal burrowing of a muddy substrate and a general lack of preserved calcareous fauna implies a low oxygen or dysaerobic zone as might be encountered on an open marine shelf, below wave base, at a depth of between 50 and 150 m (Byers 1977). Algal laminations 175 m above the base of the unit suggest a rapid shallowing of the depositional environment.

Unit 2: Medium Grained Calcareous Quartz Arenite (sample 27).

Description. The unit is six meters thick, pale orange on a fresh surface, thinly laminated to thin bedded, and porous. It forms steep ledges and has one centimeter interbeds of light green shale throughout. Two to five centimeter thick low angle tabular cross-beds of very even and regular thickness are present. Fossils were not observed.

Environmental Interpretation. The low angle of slope, long, lateral extent in outcrop, and the very even and regular thickness of the cross-beds suggest a beach environment (McKee and Sterrett 1961, Reineck and Singh 1977). Periodic pulses of terrigenous muds from an adjacent tidal flat environment may have produced the clay interbeds.

Unit 3: Bioturbated Dolomite Mudstone (samples 28 and 29)

Description. The unit is 18 m thick, black on a fresh surface, mostly thin bedded, forms prominent ledges, and is porous in the middle six meters. Shelly fauna are not present, but flat-lying algal laminations appear in the upper six meters. The unit is extensively mottled in the lower 12 m.

Environmental Interpretation. Similar to unit 1, the mottled texture indicates infaunal burrowing. The absence of calcareous fossils in a mottled sediment implies a low oxygen zone, possibly on an open marine shelf where calcareous fossils were not preserved, but where more low-oxygen-tolerant soft-bodied infauna could survive. The flat lying algal laminations near the top of the unit suggest a shallowing of the environment, possibly into the intertidal zone.

Unit 4: Solution Breccia (sample 30)

Description. The unit is six meters thick, pale yellow on a fresh surface, and forms a prominent ledge. Angular clasts of light gray dolomitic mudstone to 15 mm in diameter are suspended in a matrix of pale yellow intraclast lime grainstone. The matrix is porous, especially adjacent to the dolomite clasts.

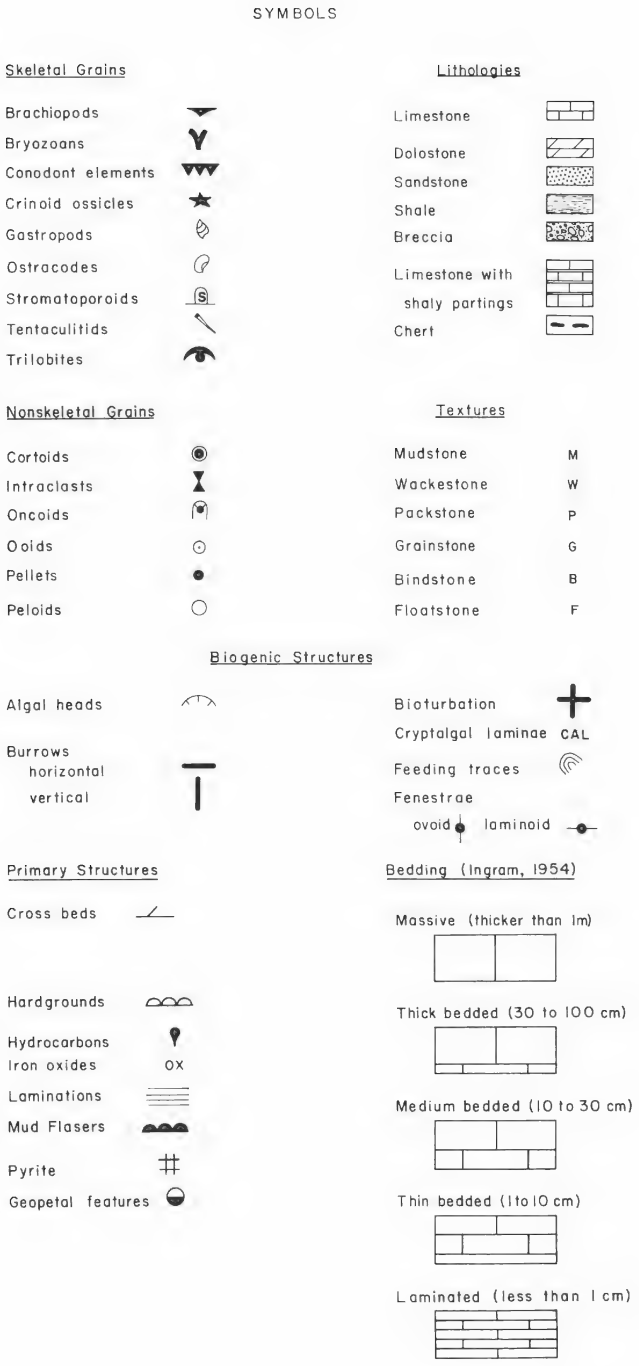
Environmental Interpretation. Unit 4 is a solution breccia, a type of collapse breccia formed as soluble minerals (carbonates, gypsum, or evaporites) are removed by solution of circulating ground water. The overlying rock fragments collapsed into the irregular solution cavities. The soluble minerals are commonly those deposited in a supratidal setting similar to Unit 5, or on a salt flat or playa. The presence of a solution breccia often implies an environment of prolonged subaerial exposure (Esteban and Klappa 1983). Features suggestive of subaerial exposure such as caliche, oxide concentrations, or paleosols were not observed.

Unit 5: Algal Lime Bindstone (samples 32 to 35)

Description. The unit is 24 m thick, black on a fresh surface, thin bedded, and forms thick ledges. Shelly fauna were not observed, however a clotted algal fabric, algal filaments, and intraclasts are common throughout the unit.

Environmental Interpretation. Monty (1976) observed that a non-layered, clotted, algal fabric is diagnostic of a supratidal environment. The presence of abundant intraclasts and an absence of preserved shelly fauna also suggest a supratidal environment.

SYMBOLS


Skeletal Grains
Brachiopods
Bryozoans
Conodont elements
Crinoid ossicles
Gastropods
Ostracodes
Stromatoporoids
Tentaculitids
Trilobites
Lithologies
Limestone
Dolostone
Sandstone
Shale
Breccia
Limestone with shaly partings
Chert
Nonskeletal Grains
Cortoids
Intraclasts
Oncoids
Ooids
Pellets
Peloids
Textures
Mudstone M
Wackestone W
Packstone P
Grainstone G
Bindstone B
Floatstone F
Biogenic Structures
Algal heads
Burrows
horizontal
vertical
Bioturbation
Cryptalgal laminae CAL
Feeding traces
Fenestrae
ovoid
laminoid
Primary Structures
Cross beds
Hardgrounds
Hydrocarbons
Iron oxides OX
Laminations
Mud Flasers
Pyrite
Geopetal features
Bedding (Ingram, 1954)
Massive (thicker than 1m)
Thick bedded (30 to 100 cm)
Medium bedded (10 to 30 cm)
Thin bedded (1 to 10 cm)
Laminated (less than 1 cm)

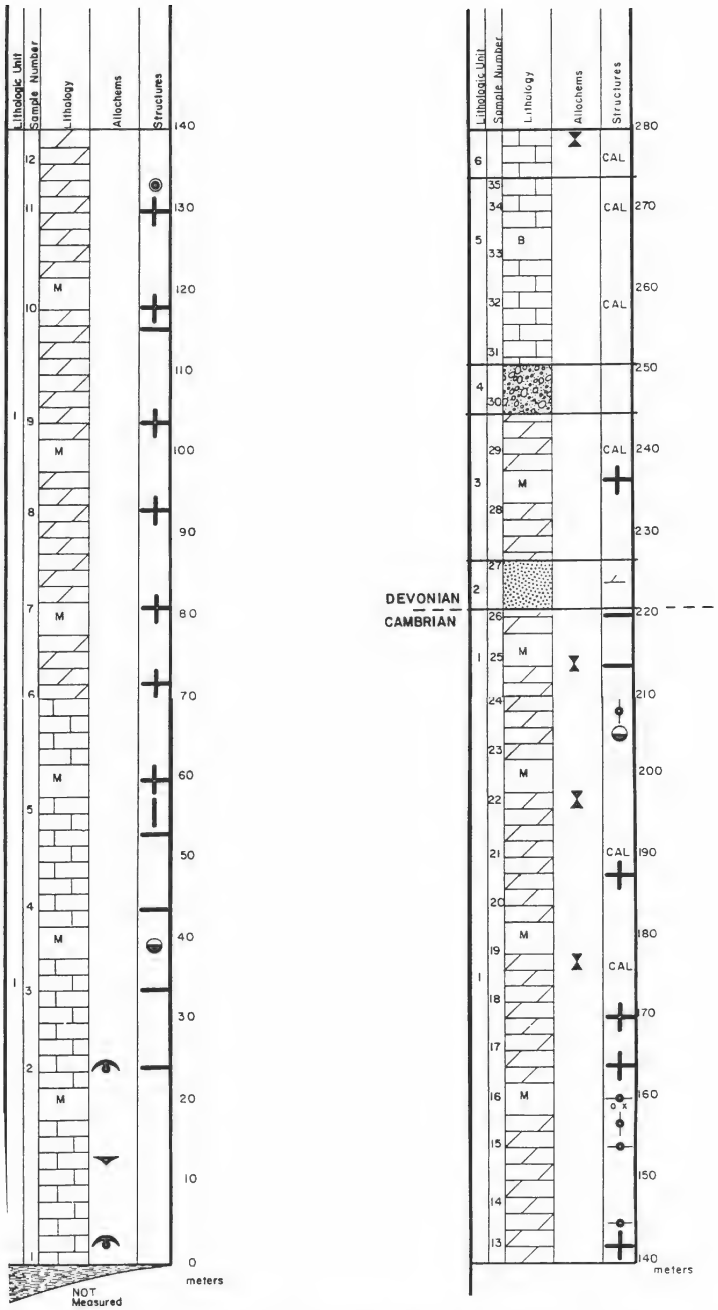


Figure 3. Graphic section at Inverted Ridge, southeastern British Columbia. Inverted Ridge has the most complete stratigraphic section of Cambrian and Upper Devonian strata in the Whitefish-MacDonald Range.

(Figure 3 continued, next page)

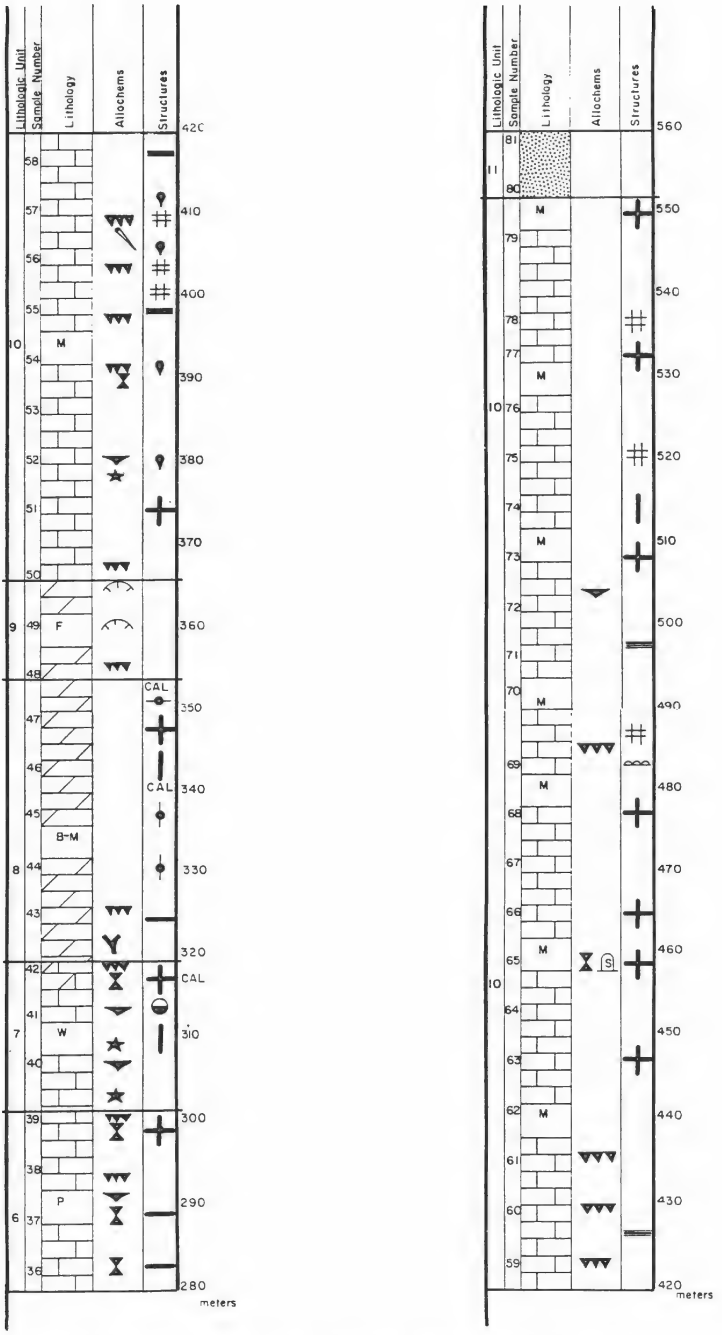


Figure 3. Graphic section at Inverted Ridge, southeastern British Columbia, continued.

(Figure 3 continued, next page)

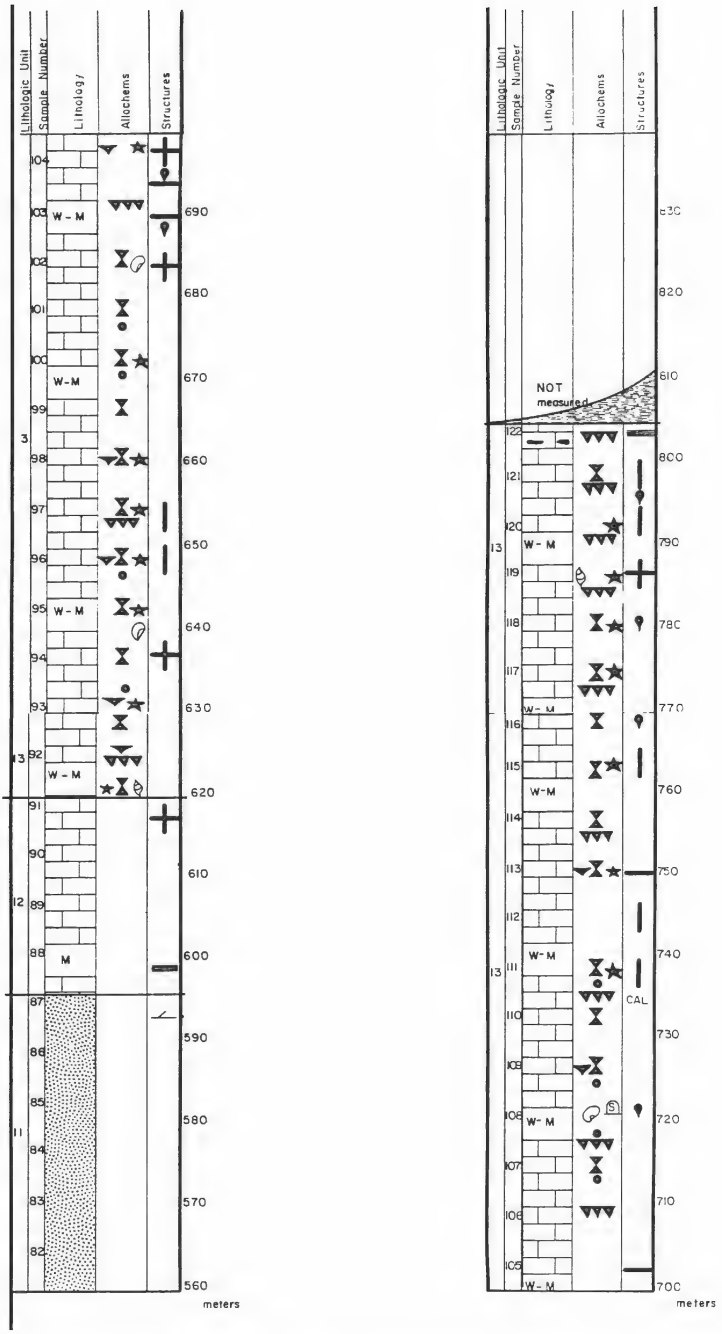


Figure 3. Graphic section at Inverted Ridge, southeastern British Columbia, continued.

Unit 6: Intraclast Lime Packstone (samples 36 to 39)

Description. The unit is 24 m thick, black on a fresh surface, thin bedded, and forms cliffs. Vugs and stylolites are present but uncommon. The unit is horizontally burrowed for the first 18 m and mottled from 18 to 24 m. Micritic intraclasts are common to abundant and frequently compacted. Rare, abraded, disarticulated crinoid ossicles, ostracodes, brachiopods, and Devonian conodont elements (*Polygnathus*) are present in the first 12 m. Flat lying, continuous algal laminations and a clotted or thrombolitic (Monty 1976) algal fabric are present in the upper six meters.

Environmental Interpretation. The intraclasts, whose formation requires some wave or current energy, and the disarticulated fauna, indicate an energetic environment. The presence of ostracodes associated with algal features, indicates a restricted intertidal to supratidal environment, possibly a cutoff lagoon or coastal pond (Flugel 1982).

Unit 7: Crinoid Brachiopod Lime Wackestone (samples 40 to 42).

Description. The unit is 18 m thick, black to dark gray on a fresh surface, thin bedded, and forms steep ledges. The unit is mottled from 12 to 18 m above the base. Intraclasts are common throughout. The unit is dolomitic at about 15 m from the base. Scattered, abraded brachiopod valves and crinoid ossicles are common throughout the unit, often concentrated in vertical burrows. Horizontal, laterally continuous algal laminations are common at 12 to 18 m. Devonian conodont elements (*Polygnathus*) are present 16 m above the base of the unit.

Environmental Interpretation. Flat lying algal laminations, the presence of burrows, calcareous fossils, and infaunal mixing of the sediments indicate an intertidal environment.

Unit 8: Cryptalgal Dolomite Bindstone-Mudstone (samples 43 to 48)

Description. The unit is 34 m thick, dark gray to brown black on a fresh surface, medium bedded, and forms cliffs. The unit has white calcite infilled laminoid and ovoid fenestrae in a clotted cryptalgal fabric. It is bioturbated, has vertical burrows to 1 cm in diameter, and contains fragmented brachiopod valves, some conodont fragments, and bryozoans throughout.

Environmental Interpretation. The clotted cryptalgal fabric indicates an upper intertidal to supratidal environment. An intertidal environment is favored, as the presence of burrows and bioturbation argue against a supratidal environment where infauna are uncommon.

Unit 9: Stromatolitic Dolomite Floatstone (samples 49 and 50)

Description. The unit is 12 m thick, gray to black on a fresh surface, medium bedded, and forms cliffs. The unit consists of isolated domal algal heads to 21 cm in diameter, out of growth position and isolated in a matrix of black dolomite mudstone. Hydrocarbon residues are common along stylolitic boundaries within the algal heads. Devonian conodont elements (*Polygnathus*) are present but rare in the mudstone.

Environmental Interpretation. Logan and others (1964), Ginsburg (1975), and James (1977) described algal structures and suggest that large algal domes represent intertidal to subtidal environments with vigorous circulation. The surrounding black mudstone indicates a much lower energy environment, below wave base, possibly a foreslope environment or lagoon. The algal heads may have been dislodged during a storm and transported to a lower energy, muddy environment by a submarine slump or turbidity current.

Unit 10: Bioturbated Lime Mudstone (samples 51 to 79)

Description. The unit is 188 m thick, black on a fresh surface, thin bedded, and a steep ledge and cliff former. The unit is intermittently burrowed and finely laminated, with uncommon mud intraclasts and rare mud flasers. Hydrocarbon residues are present from 12 to 30 m above the base of the section. Late Devonian conodont elements (*Palmatolepis*) are present throughout the unit.

Environmental Interpretation. Based on Byer's model (1977), the burrowed texture indicates a well oxygenated sediment-water layer about 50 m deep, possibly an open marine shelf, below normal wave base.

Unit 11: Medium Grained, Calcareous Quartz Siltstone (samples 80 to 87)

Description. The unit is 43 m thick, orange on a fresh surface, thin bedded, and forms very gentle slopes. The quartz grains are well rounded, well sorted, and thinly laminated. One centimeter planar cross-bed sets are present 40 m from the base of the unit. The unit has intergranular porosity. No fossils were observed.

Environmental Interpretation. The unit appears to consist of recycled grains of silt eroded from a pre-existing mature siltstone. The centimeter-thick planar cross-bed sets slope very gently, suggesting beach deposition (Reineck and Singh, 1977).

Unit 12: Laminated Lime Mudstone (samples 88 to 91)

Description. The unit is 25 m thick, light gray on a fresh surface, thin bedded, and forms ledges. Planar laminations occur from the base of the unit becomes mottled and has a distinct clotted algal texture.

Environmental Interpretation. The absence of shelly fauna throughout the unit, and only minor bioturbation within the upper portion, indicate a restricted environment, possibly within a dysaerobic zone, as within a cutoff lagoon or restricted bay, where only more resistant infauna could survive (Byers, 1977).

Unit 13: Intraclast Lime Wackestone-Mudstone (samples 92 to 122).

Description. The unit is 185 m thick, black on a fresh surface, medium bedded to massive and forms cliffs. Intraclasts are the dominant grain constituent. The unit has vertical and horizontal burrows, commonly infilled with intraclasts to two centimeters in diameter. Algal laminations and laminar encrusting stromatoporoids are present but not common. Abraded brachiopods and crinoid ossicles are abundant. Gastropods, ostracodes, oncoids, ramose bryozoans, pellets and Late Devonian conodont elements (*Palmatolepis*) are common.

Environmental Interpretation. The presence of abundant shelly fauna, oncoids, and minor algal laminations suggest a well oxygenated environment, possibly landward of a resistant stromatoporoid buildup.

Conclusions

1. This study confirms that Ordovician through Middle Devonian strata are not present in this stratigraphic section; however, Upper Devonian strata are present. Based on conodont studies and lithologic interpretations, an unconformity between Cambrian and Upper Devonian strata is recognized at the base of Unit 2.

2. Within the study area, Cambrian lithologies are dominated by bioturbated dolomitic and lime mudstone. Strongly bioturbated dolomitic wackestone and dolomitic to lime bindstone are minor. These lithologies are interpreted as having been deposited as low energy carbonates in a subtidal marine environment, below storm wave base, commonly within a dysaerobic (low oxygen) zone.

3. Devonian lithologies are composed of bioturbated dolomite and lime mudstone, algal and stromatoporoid dolomite and lime bindstone, and crinoid-intraclast dolomite and lime wackestone.

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Received 13 February 1990
Accepted for publication 30 March 1990

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Lead and Cadmium Concentrations in Mink from Northern Idaho

Abstract

The purposes of this study were to determine concentrations of cadmium and lead in mink (*Mustela vison*) in northern Idaho, to discuss potential effects, and to determine whether levels have declined. Mink (skinned carcasses) from the Coeur d'Alene River system (northern Idaho) were obtained from trappers during the 1981-82 (n = 17) and 1986-87 (n = 14) seasons. Livers of all eight mink from the uncontaminated North Fork contained low levels of lead; whereas, 9 of the 23 mink from lateral lakes adjoining the contaminated main stem, downstream from a mining-smelting complex, contained potentially hazardous lead levels (≥ 5 μg/g). Stomach contents of nine mink contained variable concentrations of lead (0.15 to 51 μg/g); samples from the main stem contained the highest values. No difference was detected in lead concentrations in livers of mink trapped from the lateral lakes in 1981-82 and 1986-87. Levels of cadmium were low in all samples, but lead levels were the highest ever recorded in mink. Our results suggest that metal pollution has probably led to localized declines in mink populations.

Introduction

Captive mink (*Mustela vison*) are sensitive to certain environmental contaminants such as polychlorinated biphenyls (Hornshaw *et al.* 1983) and methyl mercury (Aulerich *et al.* 1974); simultaneous exposure to both contaminants may result in synergistic effects (Wren *et al.* 1987). Mercury was suspected of causing declines in mink and river otter (*Lutra canadensis*) populations at a lake in Ontario, Canada (Fimreite and Reynolds 1973); however, only one verified mercury-induced mortality (an otter) was reported (Wren 1985). Mercury levels in mink were relatively low at the other collection sites in Ontario (Wren *et al.* 1986). Acid precipitation was suspected of causing a decrease in a mink population in Norway (Bevanger and Albu 1986). Although extensive residue data were recently reported, there is still uncertainty regarding effects of contaminants on populations of mink and other mustelids (Ogle *et al.* 1985, O'Connor and Nielsen 1980).

Our previous research in 1981-82 dealt with concentrations of metals in mink and other mammals from the northwestern United States; we reported elevated levels of lead in mink from the Coeur d'Alene River system (except the North Fork) that originated from an extensive mining-smelting complex on the South Fork (Blus *et al.* 1987). Most mining and smelting activities in the region ceased in 1981. During the 1986-87 trapping season, we obtained additional mink carcasses from trappers. The purposes of this paper are to determine concentrations of cadmium and lead in mink, to discuss potential effects, and to determine whether levels have declined since 1981-82.

Methods

Skinned carcasses of 31 mink were obtained from trappers working the Coeur d'Alene River system (Figure 1) in Kootenai County, Idaho; 23 mink were taken during the 1981-82 (n = 9) and 1986-87 (n = 14) seasons from Thompson Lake and other nearby lateral lakes adjoining the main stem about 40 km downstream from the main mining-smelting complex near Kellogg. Eight mink also were trapped from the North Fork in 1981-82. After storage in a freezer for several months, the carcasses were thawed, and the general condition of the specimens was noted. Samples of liver, kidney, and stomach contents were placed in nitric acid-rinsed jars and were then stored in a freezer.

The 1981-82 samples were shipped to the Patuxent Wildlife Research Center, Laurel, Maryland where they were analyzed for lead, cadmium, and several other elements; the residue concentrations (Blus *et al.* 1987) and analytical methodology previously were reported (Haseltine *et al.* 1981). For lead and cadmium analyses, tissues were homogenized in a Virtis blender. A 5g portion was placed in a Vycor crucible that was placed in a 110°C muffle furnace for 2 hr. The temperature was then increased to 550°C at a rate of 100°C/hr and samples were left to ash overnight. The cooled ash was dissolved in approximately 4 ml of nitric and hydrochloric acids over a hot plate, transferred to a 12-ml polypropylene tube, and diluted to 10 ml with distilled, deionized water. Concentrations were

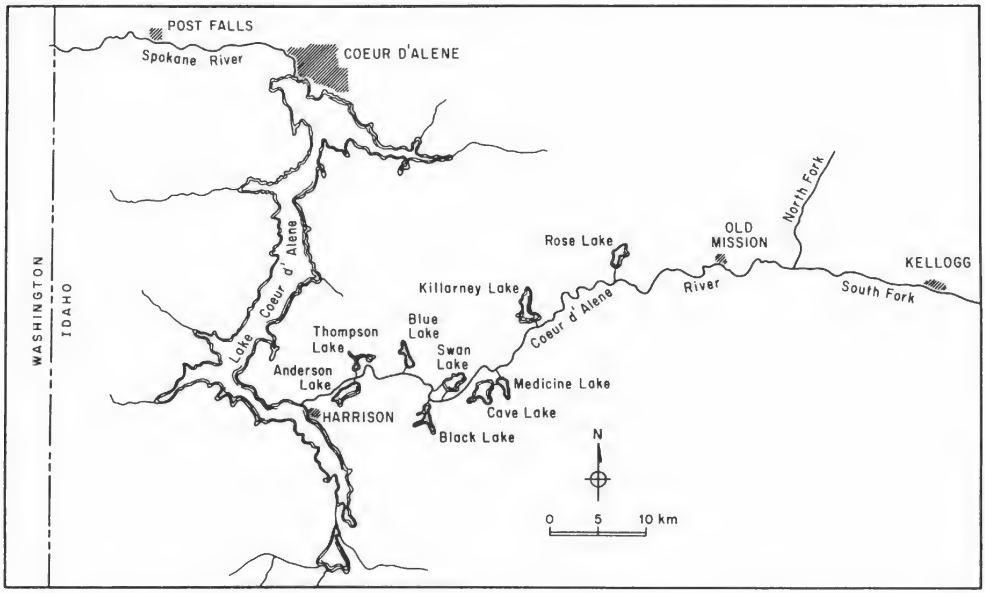

Figure 1. Map of Coeur d'Alene River system in northern Idaho where mink were trapped.

determined by comparison with aqueous standards on a Perkin-Elmer Model 1703 atomic absorption spectrophotometer. Except for the lead line of 217 mm, the standard conditions recommended by the manufacturer (Perkin-Elmer Corporation 1976) were used. Recoveries from spiked chicken livers ranged from 83 to 100 percent; concentrations were not corrected on the basis of these data. The lower limit for reportable residues was 0.10 μg/g for both cadmium and lead.

The 1986-87 samples were freeze-dried and analyzed at Environmental Trace Substances Research Center, Columbia, Missouri for lead in livers, cadmium in kidneys, and both metals in food samples. Metal levels in the 1986-87 samples were quantified by atomic absorption with a Perkin-Elmer Model 5100, Model HGA-600 graphite furnace, Model AS-60 autosampler, and a Model 7300 computer (Perkin-Elmer Corporation 1976). Dry weight concentrations were converted to wet weight based on the moisture content of each sample. All concentrations are based on wet weight unless indicated otherwise. The mean moisture content of liver and kidney samples was 72 percent compared to 75 percent for food samples. The lower limit of sensitivity (wet weight) was <0.03 μg/g for both metals. Recovery from spiked samples was 103 percent for cadmium and 102 percent for lead; concentrations were not corrected for recovery values.

Concentrations of lead or cadmium in the three collections were transformed ($\log_{10}$) and tested using one-way ANOVA; means for each metal were compared using Tukey's Q-test. When a metal was not detected, we used a value halfway between 0 and the lower limit of detection. We used linear regression analysis to examine the relationship between lead and cadmium concentrations for each of the three collections and for the entire sample. For all statistical testing, the level of significance was set at $P \leq 0.05$.

Results

Lead was detected in all samples analyzed for this element except three livers of mink from the North Fork in 1981-82 (Table 1). Mean lead concentrations in 23 livers of mink from lateral lakes adjoining the main stem of the Coeur d'Alene River were not significantly different between 1981-82 and 1986-87; however, both were significantly higher than the mean level found in eight samples from the North Fork in 1981-82. Livers

TABLE 1. Lead and cadmium concentrations in mink samples, Coeur d'Alene River system, Idaho.

Area[1]	Trapping season	n	μg/g, Wet weight Lead		Cadmium	
LIVER and KIDNEY[2]						
NF	1981-82	8	0.27(5)[3]	A	0.40(8)	A
			0.08-0.95		0.25-1.3	
			ND-3.2		0.15-1.6	
MS	1981-82	9	4.1(9)	B	0.57(8)	A
			1.8-9.7		0.21-0.75	
			0.39-22		ND-2.4	
MS	1986-87	14	3.2(14)	B	0.58(14)	A
			1.4-7.6		0.41-0.81	
			0.20-34		0.27-2.9	
STOMACH CONTENTS						
NF	1981-82	3	1.6(3)[4]		<0.10(1)	
			0.28-3.6		ND-0.17	
MS	1981-82	1	3.8		0.38	
MS	1986-87	5	3.7(5)		0.24(5)	
			0.15-51		0.12-0.46	

[1]NF = North Fork, MS = Lateral lakes adjoining the main stem.

[2]Liver analyzed for lead and kidneys for cadmium; ND = None Detected

[3]Geometric mean for liver and kidney samples and number of positive samples (in parentheses) on the top line, 95% confidence limits on the middle line, and range on the bottom line. Means for each metal were compared using Tukey's Q-test; those in the same column sharing the same capital letter are not significantly different ($P > 0.05$).

[4]Geometric mean for stomach contents and number of positive samples (in parentheses) on the first line and the range on the second line.

of mink from the lateral lakes varied in lead content; concentrations ranged from 0.20 to 34 μg/g. Lead concentrations in stomach contents also were variable and ranged from 0.15 to 51 μg/g in samples from the lateral lakes and 0.28 to 3.6 μg/g in those from the North Fork. There was a positive correlation between lead concentrations in liver and stomach contents, but the relationship was not significant. Ratios of lead in livers to stomach contents ranged from 0.1:1 to 2:1. Stomach contents of the nine mink that contained food consisted primarily of mammalian prey.

Cadmium was detected in all but three of the samples analyzed for this element (Table 1). Unlike lead, all cadmium levels were relatively low and ranged from none detected to 2.9 μg/g in kidney samples and from none detected to 0.46 μg/g in food samples. Cadmium content of kidney samples in the three collections were not significantly different from one another. Concentrations of lead and cadmium were not significantly intercorrelated either by time or place of collection or in the total sample.

Body condition, based on subjective determination of fat content, varied widely. Mink carcasses had medium to high fat content except one from the North Fork (low to medium) and one from the lateral lakes in 1981-82 (low), and four from the lateral lakes in 1986-87 (low—two and none apparent—two).

Discussion

Metal concentrations in mink from the main stem vs the North Fork resulted from the different levels of contamination. The North Fork is subject to little or no contamination with metals; whereas, the main stem is formed at the confluence of the North Fork and the heavily contaminated South Fork that flows through the major mining-smelting area near Kellogg.

Mean cadmium concentrations in kidneys of mink in this study were about double the 1.02 to 1.21 μg/g (dry weight) reported for mink trapped in Virginia from 1981-83 (Ogle *et al.* 1985) and were half to double the 0.22 to 0.87 μg/g detected in mink trapped at five sites in Ontario, Canada from 1983-85 (Wren *et al.* 1988). All of these cadmium concentrations were much lower than those associated with lethal or sublethal effects in experimental animals (Decker *et al.* 1958, Eisler 1985).

Lead concentrations of ≥10 μg/g have been associated with diagnostic lead toxicosis in experimental mammals (Osweiler *et al.* 1978); however, mammals with behavioral and physiological signs of lead intoxication have died with <5 μg/g (Zook *et al.* 1972, Clarke 1973). Captive mink have died after accidental exposure to lead (Clarke 1973), but there are no experimental data regarding the toxicity of lead to mink. Lead concentrations in livers of mink from the lateral lakes along the main stem of the Coeur d'Alene River included 5 (22%) with ≥10 μg/g and 9 (39%) with ≥5 μg/g. These animals were at risk from lead toxicosis. In the 1986-87 sample, livers of two emaciated females contained 0.22 and 5.5 μg/g of lead, while those of two males with low fat content contained 19 and 34 μg/g. In these examples, poor body condition was not

necessarily related to high lead burden. Also, our sample represented mink that were killed by trapping rather than a random sample. Dead mink have not been observed along the Coeur d'Alene River; however, other more conspicuous animals such as tundra swans (*Cygnus columbianus*) have regularly died in the area from environmental lead (Chupp and Dalke 1964, Benson *et al.* 1976).

Few samples from wild mink have been analyzed for lead; mean concentrations in livers of mink from Ontario, Canada ranged from 0.12 to 0.48 μg/g (Wren *et al.* 1988). In Virginia, Ogle *et al.* (1985) reported that only 6 percent of 125 mink livers contained detectable levels of lead with a maximum concentration of 12.7 μg/g dry weight (approximately 4 μg/g wet weight). Livers of mink from Washington State contained an average of 0.10 μg/g lead with a maximum value of 0.44 μg/g (Blus *et al.* 1987). Therefore, lead levels in mink are generally low except in localized areas such as parts of the Coeur d'Alene River system where we recorded the highest levels for this species. Avian and mammalian prey with ingested or embedded lead shot represent a hazard to some predators (Pattee and Hennes 1983), but there was no evidence of lead shot in the mink.

Lead levels in our liver and food samples of mink from the lateral lakes varied widely, indicating gradations of exposure that probably were related to different burdens of metals in these lakes that depended on the input of contaminated water from the main stem. Even during a period of unrestricted pollution of the South Fork with mining and smelting wastes, viable fish and invertebrate populations were found in a few lateral lakes but were low or absent in others and in the South Fork and main stem (Ellis 1940).

The persistence of high lead levels in the mink from the main stem are apparently related to the high concentrations in sediment and biota that are currently found throughout most of the Coeur d'Alene Lake and River system (Savage 1986). The effects of metals, particularly lead, on mink populations in northern Idaho remain unknown. Population trend data are unavailable; however, we suspect that mink are adversely affected along heavily contaminated segments of the river and some lateral lakes; mink are probably absent in the nearly denuded region around the main mining-smelting complex near Kellogg. In addition to direct toxic effects of lead and other metals, secondary effects associated with absence of food and cover are probably important.

Acknowledgments

We thank J. Nigh of the Idaho Department of Fish and Game and mink trappers for providing the specimens, O. H. Pattee and R. Eisler for critical reviews of the manuscript, and Region 1, U.S. Fish and Wildlife Service, for financial support of part of the chemical analyses.

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Received 26 September 1989
Accepted for publication 22 April 1990

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Effect of Substrate Composition and Stock Origin on the Survival to Emergence of Brown Trout: A Laboratory Study

Abstract

Few researchers investigating the survival to emergence of embryonic salmonids have simultaneously compared the predictive ability of the percentage of fine sediment less than a given diameter, the geometric mean particle size, and the fredle index. We quantified the relation between these different measures of substrate composition and survival to emergence of two stocks of brown trout, *Salmo trutta,* and also examined the effects of substrate composition on the timing of emergence and size of alevins. The geometric mean particle size generally accounted for the greatest proportion of variation in survival to emergence, whereas the percentage of fines less than a given size was usually the poorest predictor. Substrate composition also influenced days to first emergence and 50% emergence and the length of the emergence interval. We found no difference in the survival to emergence of the two stocks. We concluded that the geometric mean particle size was the best predictor of survival to emergence for brown trout and that substrate composition may alter other ecological characteristics of emerging fry.

Introduction

The survival of salmonid eggs and alevins during incubation in a stream bed is affected by several chemical and physical characteristics, including dissolved oxygen concentration (Silver *et al.* 1963), intragravel water velocity (Shumway *et al.* 1964), water temperature (Beacham and Murray 1985), and interstitial pore space (Chapman 1988). Fine sediment in substrates can directly or indirectly alter these variables and influence survival to emergence (STE) of embryonic salmonids. Because many land management practices, e.g., logging (Megahan and Kidd 1972), have caused increases in fine sediment in streams, managers have wished to quantify the relation between fine sediment and STE. Laboratory models predicting STE have been developed for several native salmonids in the western U.S., including steelhead, *Oncorhynchus mykiss,* and chinook salmon, *O. tshawytscha* (Stowell *et al.* 1983), but no models have been developed for introduced resident salmonids such as brown trout, *Salmo trutta.*

The percentage of fine sediment less than a given diameter is frequently used to represent substrate composition in STE models (see Reiser and White 1988). But fine sediment has been inconsistently defined; it has been measured as being from less than 6.3 mm (Sheridan *et al.* 1984) to less than 0.83 mm (McNeil and Ahnell 1964). Other measures of substrate composition, such as the geometric mean particle diameter (Platts *et al.* 1979) and the fredle index (Lotspeich and Everest 1980), have also been related to STE. Rarely have the three measures of substrate composition and their relation to STE been simultaneously compared (but see Tappel and Bjornn 1983).

Finally, many models predict STE of a generic stock of a given salmonid species (e.g., Stowell *et al.* 1983). Yet Morrison *et al.* (1985) found significant differences in the survival to hatch of different stocks of coho salmon, *O. kisutch,* from the Great Lakes, and Beacham and Murray (1987) noted variation in STE among stocks of chum salmon, *O. keta,* from British Columbia. Furthermore, females from the same stock but of different ages may produce eggs differing in viability. For example, Springate and Bromage (1985) noted that large females tended to produce large eggs and Bagenal (1969) implied that large eggs had yielded higher STE.

Our study had three objectives: (1) to develop a laboratory model of STE for brown trout based on substrate composition; (2) to determine which of the three measures of substrate composition

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accounted for the greatest proportion of variation in STE of brown trout; and (3) to assess the differences in STE between two stocks of brown trout.

Methods

We conducted experiments at the Red Buttes Environmental Biology Laboratory, 16 km south of Laramie, Wyoming, in experimental aquaria equipped with a horizontal flow system (Figure 1). Test substrate was placed between porous baffles in glass-walled, plexiglass-bottomed aquaria 50.8 cm long, 25.4 cm wide, and 30.5 cm deep. Baffles, consisting of a plexiglass frame covered with fiberglass screen, were positioned 7.5 cm from each end of an aquarium. Flow splitters (Mount and Brungs 1976) maintained constant flows of 1 L/min of 9°C well water at or near oxygen saturation to each aquarium. An adjustable standpipe inside a venturi standpipe controlled water depth; the venturi standpipe drew water from the lower one-third of the aquarium.

We filled each aquarium with substrate to a depth of 10 cm and constructed a centrum. Each centrum consisted of a particle greater than 50 mm in diameter topped by two or three 25-50 mm particles; this created crevices for the eggs and mimicked the structure of egg pockets (Chapman 1988). Next, we began filling each tank with water; when the water level exceeded the depth of the substrate, we poured 100 eggs into the centrum and then gently added the remaining substrate and continued filling each tank with water. The rear standpipe was adjusted to maintain a water depth of 3 cm over the substrate.

We monitored the aquaria weekly for fry until emergence began, then collected emerging fry with a suction device every 1 to 3 days until emergence ended. Each year, 300 eggs from each stock were placed in Heath incubator trays to estimate STE in a non-gravel control. Three to four weeks after emergence in the experimental treatments began, we counted all the surviving fry in the trays. All alevins from the substrate treatments were preserved in 70% alcohol. The first 10 fry to emerge from each treatment were later measured to the nearest 0.1 mm (total length).

We conducted two STE experiments, the first from 20 November 1987 to 6 April 1988 and the

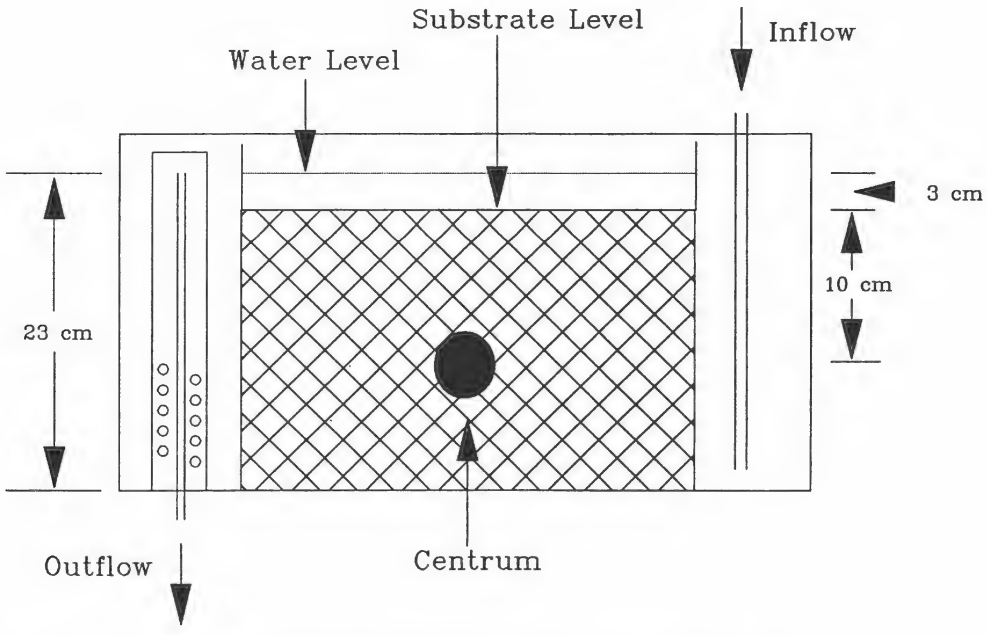

Figure 1. Side view of an experimental aquarium. Water flowed through the substrate from right to left.

second from 16 November 1988 to 31 March 1989. We devised 24 test substrates of various compositions; Young (1989; p. 55) provides the proportions of each substrate size comprising these test substrates. We used three replicates of each of 15 different test substrates in 1987, and six replicates of each of nine additional substrate mixtures in 1988. Each stock in each year was tested in three replicates of the mixtures used in those years.

In 1987 we obtained eyed eggs from the Daniel (Wyoming) State Fish Hatchery that had been taken from wild brown trout of various ages inhabiting Soda Lake in western Wyoming. This population was established from brown trout taken from Big Sandy Reservoir in southwestern Wyoming in the late 1950's; that population is speculated to have originated from the Plymouth Rock (Massachusetts) State Fish Hatchery (Richard Cheeney, Wyoming Game and Fish Department, Daniel, Wyoming, personal communication). In 1988 we obtained brown trout eggs from both Soda Lake and from a hatchery-reared stock at the Saratoga (Wyoming) National Fish Hatchery. These eggs were taken from 3-year-old hatchery fish spawning for the first time. This stock descended from brown trout at the Crawford (Nebraska) National Fish Hatchery, which had come from the Plymouth Rock Hatchery in 1980 (Jim Hammer, U.S. Fish and Wildlife Service, Saratoga, Wyoming, personal communication). The brown trout eggs from Soda Lake stock averaged 9,670 per liter and the smaller eggs from the Saratoga Hatchery stock averaged 20,830 per liter.

To assess the relation of the various measures of substrate composition to STE, we created skewed, uniform, and geometric distributions of sediment less than 3.35 mm in diameter in each test substrate (Young 1989). For example, the test substrates consisting of about 30% sediment less than 3.35 mm in diameter contained essentially no sediment less than 1.7 mm in diameter (skewed), roughly equal proportions of sediment from 1.7 mm to less than 0.212 mm (uniform), or increasing proportions of sediment from less than 0.212 mm to 1.7 mm (geometric).

To obtain substrates of different size classes, we sorted material on a mechanical shaker through sieves of 10 mesh sizes (mm): 50, 25, 12.5, 9.5, 6.3, 3.35, 1.70, 0.85, 0.425, and 0.212; smaller particles were collected on a pan attached to the last sieve. Particles larger than 6.3 mm consisted largely of alluvial material and those less than 6.3 mm largely of angular silica.

Lotspeich and Everest (1981) calculated the geometric mean substrate size for each treatment using the formula:

$$D_g = D_a^{Pa} * D_b^{Pb} * \ldots D_i^{Pi}$$

where

D_g = the geometric mean, in mm;

D_i = the mean diameter, in mm, of material retained on sieve i, and

P_i = the proportion of the entire sample made up of material retained on sieve i.

To calculate the fredle index of each substrate, we used the formula:

$$F_i = D_g/S_o$$

where

S_o = a sorting coefficient, $(D_{75}/D_{25})^{0.5}$, and

D_{75}, D_{25} = the substrate diameter below which 75% and 25% of the sample lies.

Finally, Beschta (1982) suggested that the fredle index could be improved by using the standard deviation of the geometric mean rather than a sorting coefficient. Shirazi and Seim (1979) provided a formula for the geometric standard deviation. We used the notation F_m to indicate the geometric mean divided by its standard deviation.

We assessed the effect of stock origin of eggs and substrate composition on STE, fry length at emergence, days to first emergence, days to 50% emergence, and the length of the emergence interval. Prior to any analyses, we applied the arcsine transformation (Zar 1984; p. 286) to normalize STE. To assess the effect of stock origin and the interaction between stock origin and substrate composition on the dependent variables, we conducted two-way analysis of variance using the GANOVA-4 program (Courtesy of D. G. Bonett, Department of Statistics, University of Wyoming, Laramie, Wyoming). We performed regression analyses using SPSS^x (SPSS Inc. 1986) to assess the relation between STE and substrate composition for all substrate treatments. In addition, we evaluated this relation for skewed, uniform, and geometric treatments separately. We used indicator variables in regression analyses (Neter *et al.* 1983; p. 343) of STE and substrate composition to compare the slopes and intercepts of regression lines calculated separately

for the 1987 Soda Lake stock, the 1988 Soda Lake stock, and the 1988 Saratoga National Fish Hatchery stock. We decided from the start to pool the data from both stocks and both years if we failed to reject the null hypothesis of no difference in the regression coefficients between stocks or years or both. Using only data from 1988, we conducted separate regression analyses for the two different stocks on the relation between the different measures of substrate composition and alevin size, days to first and 50% emergence, and length of the emergence interval. An alpha of ≤ 0.05 was accepted as indicating significance.

Results

The STE did not differ significantly between the eggs from two stocks of brown trout, nor did days to first emergence (Table 1). Nor was the interaction between stock origin and substrate composition on STE significant. However, stock origin was significantly related to fry length at emergence ($P < 0.001$), days to 50% emergence ($P < 0.001$), and length of the emergence interval ($P = 0.019$). Compared with fry produced from eggs of the Saratoga Hatchery stock, fry from eggs of Soda Lake stock were longer and emerged later and over a longer interval.

Substrate composition was significantly correlated with STE. In regressions of STE and substrate composition, we found no significant differences among the regression coefficients for the two stocks or between years, consequently we combined these data for further analyses. Though all measures of substrate composition were related to STE, the geometric mean accounted for the greatest proportion of the variation in STE when all treatments were pooled (Figure 2). When the treatments were divided into skewed, uniform, and geometric groups, the geometric mean performed nearly as well; only for the geometric group of treatments did another measure of substrate composition account for a greater proportion of variation in STE (Table 2).

The relation between substrate composition and the other dependent variables was determined by the measure of substrate composition and stock used in the analysis. For the stock from the Saratoga Hatchery, only the correlation between the percentage of substrate less than 1.70 mm in diameter and days to first emergence was significant ($r = 0.44$, $P = 0.02$). We found no other relation between any measure of substrate

TABLE 1. Averages of survival to emergence, fry length at emergence, days to first emergence, days to 50% emergence, and length of the emergence interval for Soda Lake (SL) and Saratoga National Fish Hatchery (SNFH) stocks of brown trout in the 1988 test (S is the skewed substrate distribution, U is the uniform distribution, and G is the geometric distribution; C is the non-gravel control).

	Substrate mixes									
	7.5% < 0.85			15% < 1.70			25% < 3.35			
Variable	S	U	G	S	U	G	S	U	G	C
Survival to emergence (%)										
SL	80.3	74.0	79.3	86.7	55.3	78.3	81.0	40.7	55.7	95.7
SNFH	88.0	87.7	79.0	70.7	58.0	73.7	78.3	40.0	27.7	92.0
Fry length (mm)										
SL	24.5	25.0	24.7	24.9	24.3	24.9	24.0	24.9	23.6	—
SNFH	22.6	22.5	22.8	23.0	22.5	21.8	22.4	22.8	22.9	—
Days to first emergence										
SL	71.7	78.0	73.7	73.0	71.0	76.0	63.0	72.3	66.0	—
SNFH	73.7	73.0	67.7	70.7	72.7	70.0	60.0	72.0	70.0	—
Days to 50% emergence										
SL	87.0	89.7	89.7	89.0	89.7	90.3	90.3	92.3	93.0	—
SNFH	85.0	83.3	81.0	85.0	85.0	84.3	81.7	87.0	84.3	—
Length of emergence interval (days)										
SL	38.7	29.7	34.3	30.7	39.3	33.0	55.3	40.7	46.7	—
SNFH	26.7	28.7	35.0	36.3	30.0	29.0	39.7	25.7	29.7	—

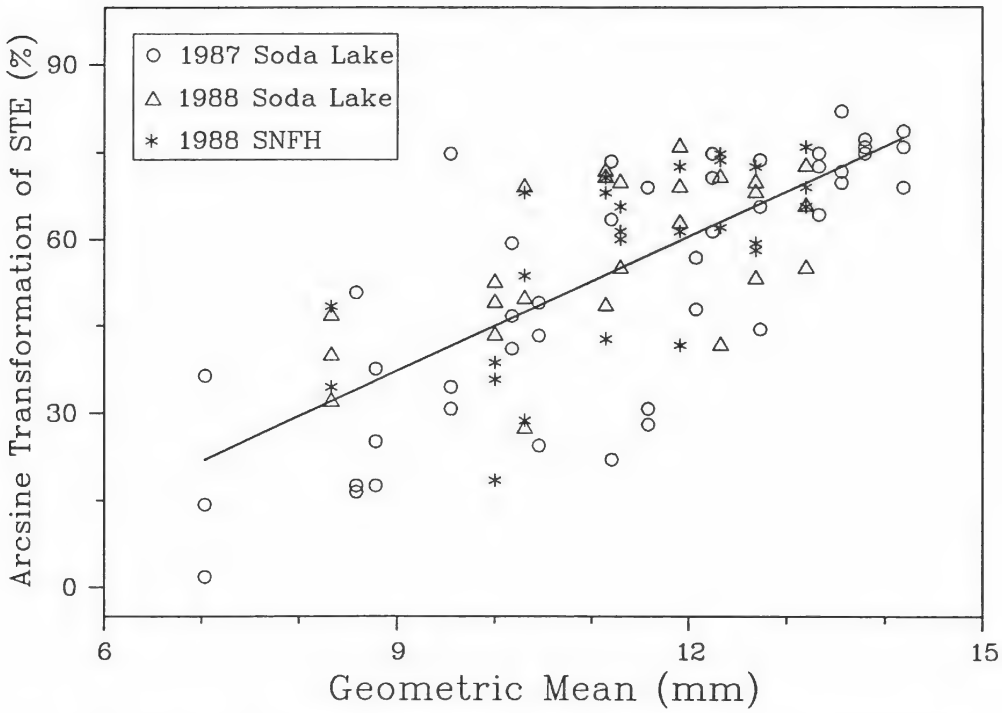

Figure 2. Relation between survival to emergence and the geometric mean particle size. The equation is arcsine (survival to emergence) = 7.75 (geometric mean) − 32.53 ($F = 112.65$, $r^2 = 0.54$, $P < 0.0001$, $N = 99$). Data are from both stocks in 1987 and 1988; SNFH is the Saratoga National Fish Hatchery.

TABLE 2. Matrix of coefficients of determination for several measures of substrate composition and the arcsine transformation of survival to emergence for all substrates and for substrates separated into skewed, uniform, and geometric categories. Data are from both stocks in 1987 and 1988 (D_g is the geometric mean, F_i is the fredle index, and F_m is the modified fredle index).

Substrate category	Substrate measure									
	Statistics			Percentage of fine sediment less than the diameter (mm) shown:						
	D_g	F_i	F_m	9.5	6.3	3.35	1.70	0.85	0.43	0.21
All	0.54	0.47	0.49	0.38	0.38	0.38	0.27	0.23	0.24	0.24
Skewed	0.55	0.49	0.45	0.37	0.36	0.37	0.14	0.10	0.15	0.16
Uniform	0.63	0.49	0.62	0.40	0.39	0.39	0.46	0.48	0.59	0.50
Geometric	0.42	0.44	0.36	0.45	0.45	0.45	0.18	0.06	0.04	0.04

TABLE 3. Correlation coefficients for measures of substrate composition and days to first emergence, days to 50% emergence, and length of the emergence interval for the eggs from Soda Lake stock in 1987 and 1988 (D_g is the geometric mean, F_i is the fredle index, and F_m is the modified fredle index). Asterisk indicates significance at alpha $\leq$ 0.05).

	Substrate measure									
	Statistics			Percentage of fine sediment less than the diameter (mm) shown:						
Variable	D_g	F_i	F_m	9.5	6.3	3.35	1.70	0.85	0.43	0.21
Days to first emergence										
	0.23	0.36*	0.06	−0.45*	−0.45*	−0.45*	−0.11	−0.07	−0.09	−0.09
Days to 50% emergence										
	−0.41*	−0.41*	−0.41*	−0.05	−0.05	−0.05	−0.15	−0.18	−0.17	−0.17
Length of the emergence intervals (days)										
	−0.31*	−0.39*	−0.21	0.33*	0.33*	0.33*	−0.14	−0.15	−0.10	−0.10

composition and alevin length, days to first emergence, days to 50% emergence, or length of the emergence interval. But at least three measures of substrate composition were significantly correlated with days to first and 50% emergence and length of the emergence interval for the Soda Lake stock (Table 3). Again, no measure of substrate composition was significantly correlated with fry length at emergence.

Discussion

The geometric mean diameter of the substrate consistently accounted for the greatest proportion of the variation in STE. However, the fredle index and modified fredle index often explained nearly as much of this variation. Chapman (1988) favored the fredle index over the geometric mean, but his analyses revealed few substantial differences in the predictive ability of the two measures. Also, Lotspeich and Everest (1981) suggested that a single value of the geometric mean could represent several different values of the fredle index, and therefore concluded that the fredle index was more sensitive to changes in substrate composition. But substrates of differing composition can be represented by a single value of the fredle index and several values of the geometric mean as well. Unless additional research reveals major differences, we prefer to geometric mean as a measure of substrate composition in models of STE due to its predictive ability, computational simplicity, and widespread use by fluvial geomorphologists (Platts *et al.* 1979). However, we do not recommend that the equation for STE of brown trout be considered a quantitative predictor of STE in the field, due to the artificiality of the substrate treatments, the control of other variables important to STE (such as intragravel water velocity and dissolved oxygen), and the lack of model validation under natural field conditions.

Despite its popularity, the percentage of fine sediment less than a given diameter was the poorest predictor of STE in most tests. Though smaller-sized sediment may reduce STE to a greater extent than larger sediment (Reiser and White 1988), it appears that the overall substrate composition has a greater influence on STE (cf. Chapman 1988). Models of STE based on the percentage of one or more sizes of fine sediment can be informative (e.g., Tappel and Bjornn 1983), but the applicability of these models to substrates containing similar proportions but different distributions of the selected sizes of fine sediment is unknown. Finally, the percentage of fine sediment less than 3.35 mm did account for a marginally greater proportion (3%) of the variation in STE than did the geometric mean particle size for the geometric group of substrate treatments. That group of substrate treatments has a bimodal particle distribution that may be poorly represented by the geometric mean. Consequently, we encourage additional comparisons of measures of substrate composition in laboratory and field experiments.

Surprisingly, we found no significant difference in the STE of eggs from two stocks of

brown trout, despite the disparity in egg size and female age. Previous studies have demonstrated greater STE of large (Bagenal 1969) or small (Beacham and Murray 1985) eggs. Furthermore, survival to hatch of eggs of coho salmon from a Lake Erie stock was significantly greater for eggs taken from large females than for those taken from small females (Morrison *et al.* 1985). We assessed the STE of the eggs from the two stocks over a relatively narrow range of substrate compositions. Additional tests over a greater range of substrate compositions might reveal differences in the STE of eggs from these two stocks.

A reduction in geometric mean particle size of substrates significantly accelerated the timing of peak emergence and lengthened the emergence interval. Olsson and Persson (1986) also demonstrated that the time to 50% emergence increased and the length of the emergence interval decreased as the proportion of fine sediment in substrates decreased. Witzel and MacCrimmon (1983) reported an increase in the time to 50% emergence as mean particle size increased, but noted that the length of the emergence interval also increased. However, the increases may be attributed to very low STE in treatments containing large proportions of fine sediment i.e., the emergence interval is likely to be short when few fry emerge. Alternatively, substrates of low mean particle size may induce synchronous premature emergence by restricting delivery of dissolved oxygen. Fry acquire oxygen much more efficiently than eggs, and eggs under stress due to low dissolved oxygen hatch prematurely into fry that assume a free-swimming existence while still carrying a large yolk sac (Bams 1969). Thus synchrony of emergence may exist at two different stages of embryonic development in response to the intragravel environment.

Acknowledgments

We thank J. Bobbitt for monitoring portions of the tests, D. Lanning and P. Guenther for assisting with the initiation of the 1988 test, the Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service for providing eggs, and P. Eschmeyer for reviewing the manuscript.

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Received 11 October 1989
Accepted for publication 3 May 1990

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RESEARCH NEWS AND COMMENTS

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Athens, Georgia 30602

The Clarkia "Fossil" Leaves: Windows to the Past

About an hour's drive out of Moscow, Idaho, towards the town of Clarkia, is a motorbike race track, called appropriately enough, the Fossil Bowl. The excavation of the track in 1972 by Mr. Francis Kienbaum, the owner of the property, unearthed a rare and remarkable fossil site later to be called the Clarkia Flora. A call to the nearby University of Idaho brought out a geologist, Dr. Charles "Jack" Smiley, who marvelled at the preservation of the fossil plant specimens and realized the scientific value of the site. His subsequent efforts to bring other scientists to study the site would lead to more than fifteen years of work and publications on this fossil flora.

In the summer of 1978, I visited the site with my colleague, Dr. Karl Niklas, a paleobotanist. Karl and I had just published on the chemical and ultrastructural preservation of green leaf compression fossils of the Miocene Succor Creek Flora of Oregon. These compressed leaves represented original green leaves preserved in the desiccant-like volcanic ash. Jack Smiley, hearing of our work, invited us to view the Clarkia site, with its profusion of equally well preserved and more accessible fossil leaf compressions.

As I stood at the Clarkia site, I turned and looked out over a quiet valley of green pastures growing over what had been a secluded bay of a Miocene lake bed, its age recently confirmed by potassium/argon isotope dating. Twenty million years ago the lake had been surrounded by deciduous trees including sycamores, oaks, chestnuts, tulip poplars, zelkovas and elms as well as evergreen trees including *Metasequoia glyptostroboides* (Dawn Redwood) and species of *Magnolia.* The closest living relatives of many of the Clarkia fossils now occurred only in the southeastern United States or more distantly in southern China.

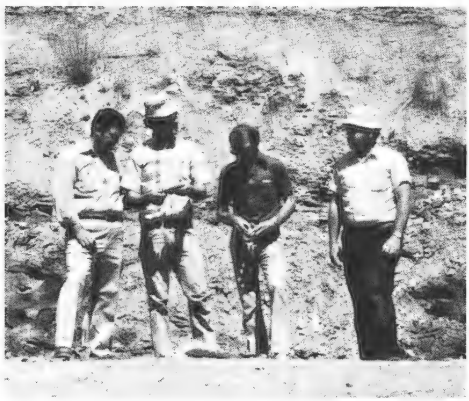

Figure 1. The author (far left) standing before the Clarkia site during the first visit in 1978, discussing a fossil specimen with (from left to right), W. Rember (graduate student), Dr. Jack Smiley (site manager) and M. Huggins (graduate student).

Clarkia Lake had been formed by the blocking of what is now the St. Mary's River drainage by catastrophic volcanic activity. The lake apparently had been deep, cold and experienced little disturbance by strong currents such as in spring fed lakes. The lake probably lasted only a thousand years before filling in to form the valley before me. The Clarkia fossils are not torn or sheared but repose in the lacustrine shale matrix as if neatly laid and carefully covered with many layers of fine silt. The ease in prying the soft layers apart and exposing the fossils contrasts with the rock-like preservation of the Succor Creek specimens. The stark preservation of the Clarkia leaves in the cold, oxygenless sediments of the ancient lake was mirrored in the preserved original colors of the leaves, dark black greens, autumnal reds and browns and even a

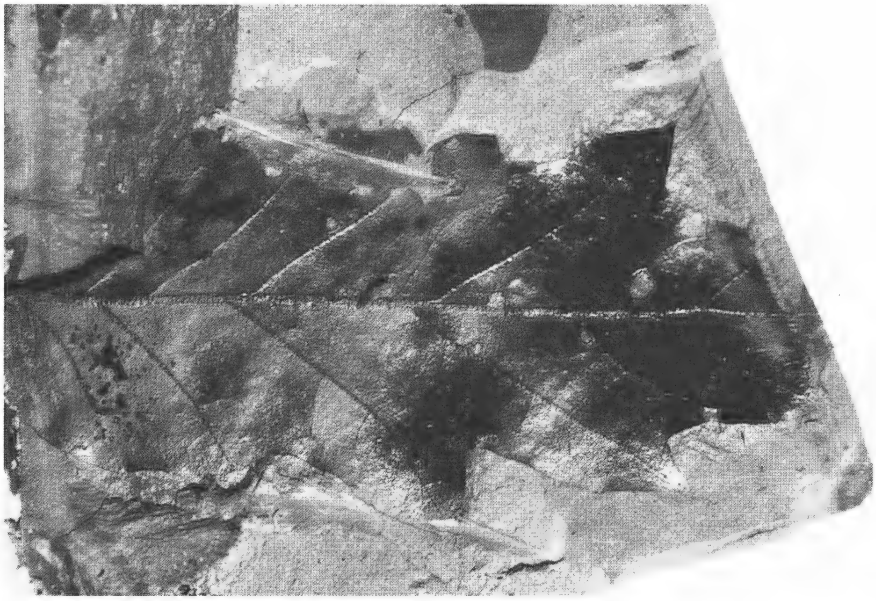

Figure 2. Fossil oak species in freshly opened sediment layer. Note original sediment water layer on the fossil compression. Courtesy of K. J. Niklas.

film of moisture from the original lake water. With little apparent bacterial decomposition the internal cell wall, vascular tissue and chloroplast structure had also been preserved, unlike true fossils where the organic parts of the plant are replaced by inorganic minerals, much like petrified wood. Karl, Jack and I were to work on the paleochemotaxonomy of these fossils until the mid 1980s.

Late that fall of 1978, a Georgia colleague of mine, Dr. Michael Clegg, fascinated by the preservation of the many pigments, steroids, fatty acids and phenolics in the fossils, asked if DNA itself might also be present in these fossils leaves. I thought it highly likely. However, appropriate technology was unavailable at that time to exploit the possibility. By 1985, Clegg had left for the University of California, Riverside, and I was preparing to retrain in the molecular biotechnology which was becoming available to systematic and evolutionary biology. An invitation from Mike Clegg and his colleague, Gerard Zurawski, to learn the new technology in exchange for my taxonomic expertise in applying such data to taxonomic and evolutionary studies, soon had me on my way to their California laboratories in fall, 1987.

At the end of my sabbatical in March 1988, Mike Clegg and I again discussed the possibility of sampling Clarkia fossils for DNA with the new biotechnology. I called Jack Smiley and arranged for a new trip to the fossil site in July 1988. After our arrival, Mr. Keinbaum's son bulldozed away the loose soil, exposing fresh layers of lucustrine shale containing the fossil leaves. Mike Clegg and Jack Smiley pulled out the fossils which I then photographed. After identification by Jack, Mike's two technicians, Mary Durbin and David Henderson, immediately scraped the leaf off the shale into a buffered extraction solution using the portable field lab set up at the site within a few feet of ongoing bike races. The extracts were stored on ice for transport back to Riverside. A farewell dinner with Jack Smiley and his wife, Peg, capped a most pleasurable field trip.

By September 1988, Dr. Ed Golenberg, a post-doctoral research associate working with Mike Clegg at Riverside, called—DNA in small quantities was preserved in many of the 54 fossils

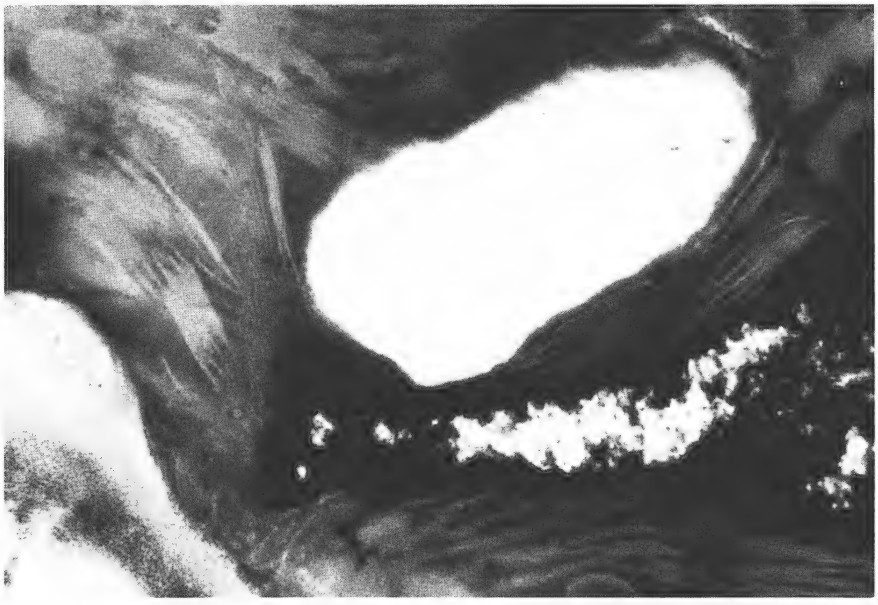

Figure 3. Electron micrograph of cell cytoplasm of birch leaf (*Betula*). Note chloroplast membranes in lower right corner. Courtesy of K. J. Niklas.

we had collected—elation and cautious optimism.

At that time, a new technique called the polymerase chain reaction (PCR) became available which allowed for the duplication and amplification of small amounts of DNA to thousandfold amounts. By June 1989, Ed Golenberg had amplified, recovered and sequenced a large portion of a gene from a fossil *Magnolia.* The gene, called *rbc*L, is the large subunit of the chloroplast gene, RuBisCo, which codes for a major photosynthetic enzyme in the chloroplast. The gene was chosen because it is produced in large quantities in all green photosynthetic plants, making it more likely to be found in the fossil. Also, it is a slowly evolving gene which would give us a conservative look at evolution between the fossil and its living relatives. Numerical analysis of the sequence of nucleic acid bases of the fossil gene and that of its relatives confirmed the fossil to be a magnolia and that the fossil gene differed by only 17 nucleic acid bases from its nearest living relative. Our paper submitted to *Nature* in December, 1989, was accepted in February, 1990—jubilation.

"What is the significance of this work?" the reporter asked. Caught up in the race to be the first to report on this startling work, it took a moment or two to put it all in perspective in terms of the real world. First, it was the oldest DNA *ever* recovered and sequenced. Second, we could now look back down the tree of evolution in vertical geological time to see where plant species diverged. Previous plant phylogenies

Figure 4. Dr. Jack Smiley, geologist (left center) explains the history of the Clarkia site to Dr. Mike Clegg (right center) and his technicians, David Henderson (left) and Mary Durbin (far right).

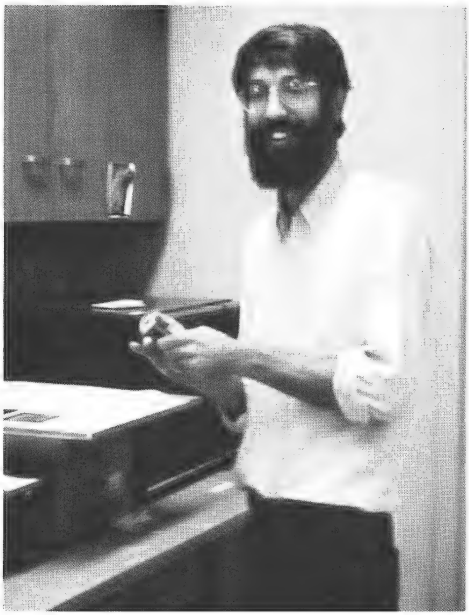

Figure 5. Dr. Edward Golenberg, who carried out the PCR amplification and sequencing of the DNA from the fossil *Magnolia*.

were based primarily on horizontal comparisons of living plants representing only the tips of the tree of evolution. Third, the analysis could be repeated with many other fossil species to compare rates of gene evolution. Fourth, the age of the fossil in millions of years is meaningful enough to allow scientists to use these rates to "set" the biological clock to calculate gene evolution in geological time rather than estimating from differences between contemporary species. In practical terms scientists involved in genetic engineering might now be able to predict how long transplanted genes and desired characteristics would remain stable in plants. Finally,

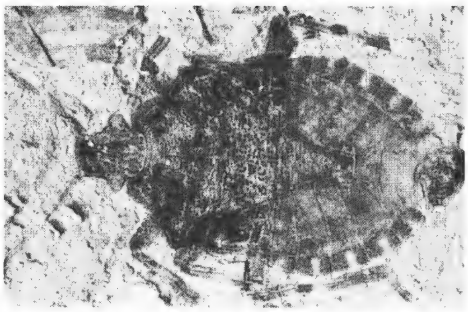

Figure 6. A fossil insect compression also found in the Clarkia sediments.

DNA, the ultimate evolutionary code, can unequivocally establish taxonomic and evolutionary relationships between plants, a significant taxonomic goal and equally important in choosing likely compatible genetic stocks for breeding programs.

"What are your future plans?" the reporter then asked. First, we intend to expand the surveys at Clarkia, especially with other scientists, to see if the rate of DNA base changes or substitutions is the same in all fossil species or does it differ from species to species. Perhaps other scientists will want to examine the fish and insects preserved in the Clarkia sediments. Also, we hope to locate older sites allowing us to push the geological reference points further back in time. The work establishes a new field, which we term paleomolecular evolution, using the "chemical bones" of the fossil DNA to establish precise evolutionary relationships between living and ancient plants. Most intriguing is that a modern technology gives us access to information uniquely preserved twenty million years ago when man himself had barely begun his formative ascent towards emergence as a rational organism.

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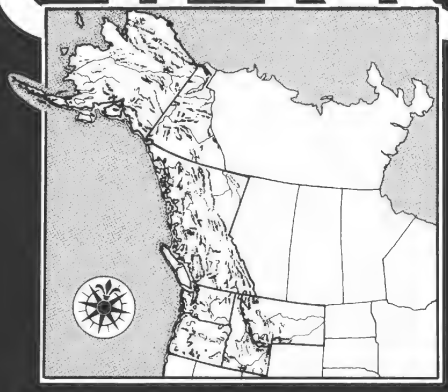
November 1990 Volume 64, Number 5

NATURAL DISASTERS
Symposium: The Nature of Recovery

NORTHWEST SCIENCE



CONTENTS

Environmental Disasters: The Nature of Recovery

Announcements

237 Introduction to the Symposium: Environmental Disasters: the Nature of Recovery—**Nan C. Vance and Mark V. Wilson**

239 The Yellowstone Fires of 1988: Natural Process and Natural Policy—**Ronald H. Wakimoto**

243 Early Development of Vegetation Following Holocaustic Fire in Northern Rocky Mountain Forests—**Peter F. Stickney**

247 Biological Effects of Petroleum Hydrocarbons: Predictions of Long-term Effects and Recovery—**Judith McDowell Capuzzo**

250 Regional Vertical Tectonic Displacement of Shorelines in South-central Alaska During and Between Great Earthquakes—**George Plafker**

259 Plant Succession on Earthquake Uplifted Coastal Wetlands, Copper River Delta, Alaska—**John F. Thilenius**

263 Mount St. Helens Ten Years Later: Past Lessons and Future Promise—**Peter M. Frenzen and Charles M. Crisafulli**

268 Recovery of Lakes in the 1980 Blast Zone of Mount St. Helens—**Robert C. Wissmar**

271 The Role of Refugia in the Recolonization of Streams Devastated by the 1980 Eruption of Mount St. Helens—**Charles P. Hawkins and James R. Sedell**

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CONTENTS

Environmental Disasters: The Nature of Recovery

Announcements

237 Introduction to the Symposium: Environmental Disasters: the Nature of Recovery—**Nan C. Vance and Mark V. Wilson**

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Announcements

In This Issue

Thanks to the editorial efforts of Nan C. Vance and Mark V. Wilson, we are able to bring together in this issue of *Northwest Science* papers centered upon the common theme of environmental response to natural catastrophes. This was the topic of the symposium, "Environmental Disaster: The Nature of Recovery," held at the annual meeting of the Northwest Science Association at Oregon State University in March 1990. These are some of the papers to come from that symposium. Although these papers touch upon the biological to the geological, I hope you will find their common focus an added bonus.

—*Editor*

1991 Annual Meeting of the Northwest Scientific Association

The Northwest Scientific Association will hold its 64th annual meeting on March 20-22, 1991 at Boise State University in Boise, Idaho. Symposia topics will highlight "Science and Land Use in the Intermountain West," "Venomous Snakes," and "Molecular Approaches to Ecological Problems." In addition to these symposia, the NSA will present contributed papers and student research grant awards, will recognize an Outstanding Northwest Scientist, and will offer field trips to the World Center for Birds of Prey and to the Birds of Prey Natural Area.

The deadline for abstract submissions is January 25, 1991. Early registration for the meeting is March 1. Students are equally encouraged to submit abstracts. Abstracts of all papers presented at the meeting will be formally published in a supplemental issue of *Northwest Science.*

For additional information, contact Robert Rychert, Program Chair, Biology Department, Boise State University, Boise, Idaho 83725 (208-385-3262).

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ENVIRONMENTAL DISASTERS: THE NATURE OF RECOVERY

The symposium *Environmental Disasters: The Nature of Recovery* was held at the 63rd annual meeting of the Northwest Scientific Association, March 21-23, 1990, at the LaSells-Stewart Center on the Oregon State University campus in Corvallis, Oregon. This issue of *Northwest Science* is dedicated to presenting some of the papers contributed at that symposium. This special issue has been compiled and edited by Mark V. Wilson (Associate Professor of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon) and Nan Vance (USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon).

CONTENTS

Environmental Disasters: The Nature of Recovery

237 Introduction to the Symposium: Environmental Disasters: the Nature of Recovery—**Nan C. Vance and Mark V. Wilson**

239 The Yellowstone Fires of 1988: Natural Process and Natural Policy—**Ronald H. Wakimoto**

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Introduction to the Symposium: Environmental Disasters: the Nature of Recovery

What we call "disasters" are a part of life, for the environment as well as for humans. Holocaustic fires, massive oil spills, volcanic eruptions and earthquakes have alarming consequences. But are they always disasters? It is instructive that in Chinese philosophy, crisis is also regarded as opportunity. Great environmental disasters may provide opportunities not only for nature, but for scientists as well. In the past, the temptation for scientists has been to treat unexpected cataclysmic events as interesting but extraneous, best ignored as deviations from the norm. Now scientists are recognizing that we cannot afford to neglect these events and their ecological effects. Infrequent but massive environmental changes caused by disasters create patterns of ecosystem recovery that often redistribute species, set the productivity of forests and fields, and reshape the landscape.

How do natural systems respond to such major disruptions, and how are natural ecological processes altered not only by the disturbance but also by human intervention? The papers in this special edition of *Northwest Science* help resolve these issues. Each paper summarizes a presentation delivered at a symposium held during the Northwest Scientific Association Sixty-third Annual Meeting in Corvallis, Oregon, March 21, 1990. The symposium, "Environmental Disasters: The Nature of Recovery," was held to explore the impact of several environmental disasters that occurred in the northwestern United States.

The symposium covered three major kinds of "disasters." Earthquakes and volcanic eruptions, which are beyond human control, are totally natural and profoundly affect the landscape for some distance, as exemplified by the 1964 Alaskan earthquake and the 1980 eruption of Mount St. Helens. Holocaustic wildfires are another kind of disaster which, although natural in many instances, are also influenced by human intervention. Oil spills, such as the Exxon Valdez, exemplify a disaster which is entirely "unnatural" or human caused.

In the case of the Yellowstone fires, has human interference assisted or hampered natural processes? Ronald H. Wakimoto, forestry professor, University of Montana, and technical advisor to the Fire Management Policy Review Team, discusses in his paper fire management policies at Yellowstone National Park. He contends that prescribed natural fires in the Northern Rocky Mountain region are necessary to maintain the health and naturalness of the forests which have been ecologically shaped by frequent fires. At the same time, prescribed natural fires prevent out of control wildfires that endanger humans and their property. That fire is a natural phenomena is supported by Peter Stickney, research botanist at the U. S. Forest Service, Forestry Sciences Laboratory in Missoula, Montana. He has studied the patterns of succession following wildfires in the Northern Rockies for over 25 years. Stickney's paper describes the successional processes of plants following holocaustic wildfires, "the principal and most extensive initiator of forest succession in the region for at least several thousand years," as an orderly process based on the life form of the surviving plants, and the proximity and opportunities of colonizers' seed. Their papers leave an ironic implication: fire suppression may disturb Northern Rocky Mountain ecosystems more than natural, frequent fires.

Forest fires occur with or without human intervention. In contrast, oil spills that alter the environment in totally new ways are exclusively human caused. How do natural systems respond to such disturbances? Is oil a contamination to which the biota's adaptive mechanisms are not well developed, if they exist at all? As oil spills occur with greater frequency, answers to the question of recovery and resiliency of marine biota become increasingly crucial. Judith McDowell Capuzzo, a

marine toxicologist from the Woods Hole Oceanographic Institution, writes a caution in her paper. While there is evidence of immunity and detoxification ability in certain adapted organisms, recovery appears to depend primarily on the disappearance of the contamination. Long term, sublethal biological effects are not well understood. Capuzzo asserts that a multi-disciplinary approach and long term research are needed to achieve sufficient understanding of the persistence of the pollutants and the marine populations affected.

The great earthquake off the coast of Alaska in 1964 was just another recurring consequence of the Pacific oceanic crust trying to thrust itself under the Alaskan continental margin over thousands of years, according to geologist George Plafker, U.S. Geological Survey. Plafker describes the nature of this cataclysmic event and sets the stage for the response of natural processes to the provision of new habitats. The earthquake uplifted the Copper River delta literally creating new land surfaces and tidal regions. John F. Thilenius, retired U.S. Forest Service ecologist, studied the successional processes following the earthquake. His paper is a descriptive account of how herbs, shrubs and marshes occupied and advanced to new sites dictated by their abilities to adapt and use the conditions created by the newly uplifted land mass. It is a unique model for understanding change and movement of land and biota where the norm is more dynamic than static.

Another natural event that profoundly affected the landscape was the eruption of Mount St. Helens ten years ago. Scientists have been tracking the individual components of ecosystems including lakes, rivers, animals, microorganisms and plants, and tying these together to create an understanding of the ecosystems of Mount St. Helens and how they were affected by, and responded to, this event. Peter Frenzen and Charles Crisafulli, researchers at the Mount St. Helens National Volcanic Monument, have provided an overview of the volcanic eruption and the studies that have followed. Microbiologists, limnologists, botanists and ecologists have seized this unprecedented opportunity to study evolutionary processes and better document the dynamics of succession. Botanists are finding plant survivors following the eruption are as important to the speed and success of recovery as plants survivors of fire. Robert C. Wissmar, researcher at the Fisheries Research Institute, University of Washington, outlined the recovery characteristics of lakes altered or created by the eruption. The presence of surviving microorganisms provided the initial impetus for continued microbial succession. Over time the lakes have recovered sufficiently to be inhabited by more complex aquatic communities. The role of refugia is an interesting feature of the stream recovery process. Charles Hawkins, fisheries researcher from Utah State University, and James Sedell, ecologist with the U.S. Forest Service, PNW Research Station, describe the nature and role of refugia in streams and rivers impacted by massive flows from the eruption. Such features as snags and other debris, or physical streambed characteristics provide habitat protection for fish that could serve as a starter population for fish recovery.

The papers presented in these proceedings highlight research on the patterns and processes of recovery from four major disasters that occurred within the past thirty years. A common finding was that regardless of the nature of the disaster, a remnant of survival is important to recovery. Much biological recovery is faster than was thought possible, but in the case of hydrocarbon pollutants, the prospects for long-term recovery of marine biota is still unknown. Continued, coordinated research is necessary to further our understanding of these processes. Ultimately, as a consequence of such research, we should be able to predict and more efficiently aid recovery. At the very least, we will appreciate more the extent to which nature can recover on her own from massive environmental disruptions we call "disasters."

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The Yellowstone Fires of 1988: Natural Process and Natural Policy[1]

The public outcry about the 1988 fires in Yellowstone National Park and adjacent national forests, coupled with concern among natural resource managers, convinced the Secretaries of the Departments of Interior and Agriculture to establish the Fire Management Policy Review Team in the latter part of September 1988. This team, composed of representatives from the U.S. Forest Service, National Park Service, Bureau of Land Management, Bureau of Indian Affairs, and the U.S. Fish and Wildlife Service, was charged with reviewing current policies governing national park and wilderness fire management in these federal agencies and recommending any changes needed to correct problems encountered during the 1988 fire season.

I was asked to serve on the team as a member representing the academic community, along with Dr. Robert G. Lee from the University of Washington. We were also joined by representatives from the National Association of State Foresters, the National Fire Protection Association and the Western Governors Association. Unfortunately, the "non-federal" representatives soon learned that the Department of the Interior had decided we couldn't be considered official team members because of qualifying provisions of the Federal Advisory Act; we were thus designated "technical advisors." The team itself chose to ignore this rather arbitrary distinction, and everyone was allowed to participate as full members, although the names of the "non-federals" do not appear on the team's final report.

The team was directed to review fire policy "to determine the appropriate fire policies for national parks and wildernesses which addresses the concerns expressed by citizens and public officials about the management of fire on these lands as a result of the Yellowstone situation." We began with the premise that we were to focus on fire management policies, not on the overall management direction of national parks and wilderness areas.

The Natural Fire Policy Review Team condensed the voluminous material it considered into 17 findings, which were then summarized as the following seven issues.

1. The objectives of prescribed natural fire (PNF) programs in national parks and wilderness areas are sound, but the policies need to be refined, strengthened and reaffirmed. These policies permit fires to burn under predetermined conditions.

A *prescribed* fire, whether manager- or lightning-ignited, is considered a wildland fire burning under predetermined conditions to achieve preplanned land or resource management objectives. Thus, areas where the management objective is to maintain ecosystems unaffected by human influences and manipulation—that is, where plants and animals can develop and respond to natural forces—can be managed with PNF management plans. In these areas, lightning-caused fires are allowed to burn under defined conditions designed to achieve management objectives. If a fire exceeds the prescription because of changing weather conditions or by threatening life or property or moves onto land not included in a fire management zone, it is designated a wildfire, and the responsible agency is required to take appropriate suppression action. Wildfire cannot be used to accomplish management objectives such as habitat improvement or plant diversity maintenance.

If a fire cannot be classified as a prescribed fire, either because it occurs outside predetermined conditions or because it does not meet preplanned objectives, it is declared a *wildfire,* and the responsible agency then has the options of confining, containing or controlling it. To confine a fire is to limit fire-spread within a predetermined area, principally by using natural or preconstructed barriers or environmental conditions. Suppression activity is minimal and is often limited to surveillance. Should conditions indicate that the fire might cross barriers, another strategy must be used. To contain a fire is to surround it with control line, as needed, when this tactic can reasonably be expected to prevent fire-spread under the current and predicted fuel and weather conditions. This option allows more fire-line extension as necessary. Finally, to control a fire is to complete the fire line around the fire. Unburned areas within and adjacent to the fire line are burned out.

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-23, 1990, Corvallis, Oregon, Mark V. Wilson and Nan C. Vance, editors.

These options give the federal agency some latitude: It can opt for vigorous, direct control to protect valuable resources, or it can choose containment or confinement to protect resources from suppression activities that could be more harmful than the fire itself. Policy calls for daily review of the selected strategy to ensure that it is appropriate for the predicted weather.

2. Many current fire management plans do not meet current policies; the prescriptions in them are inadequate; and decision-making needs to be tightened.

The fire policy review team discovered that the only fire management plans that did not meet current policies were National Park Service plans. Some Park Service plans contained no criteria or written prescriptions under which fires may be allowed to burn as prescribed fires, nor were there any criteria about how to judge whether a fire should be considered a prescribed fire or a wildfire. Without written prescriptions, fire managers could not even compare the fire weather of one year with the fire weather of the next. In 1988, most U.S. Forest Service fire management plans in the Greater Yellowstone Area contained prescription criteria that were reached or exceeded by the end of the month of June. In other words, fire danger as related to weather and fuel moisture conditions had exceeded the 90th percentile of fire danger conditions recorded over the last 20 years for the area in and around the Park.

The Yellowstone National Park plan stood out as a particularly bad example of this lack of compliance to national fire policy. A comparison of different agency actions in the Greater Yellowstone Area is presented in Table 1. Note that only 31 fires out of a total of 249 fires were originally designated PNFs. During the 1988 fire season, Yellowstone Park designated 28 of 50 ignitions as prescribed fires; 16 of these were later declared wildfires. At the same time, the Bridger-Teton and Custer National Forests, whose fire plans include written prescriptions, each designated one prescribed fire out of 45 ignitions. The team was surprised to find that the Yellowstone fire management plan used in 1988 was never approved by the NPS Regional Director as specified in NPS fire policy. Grand Teton National Park, which also has a plan outlining written prescriptions, allowed one prescribed fire, which burned out at less than an acre, and suppressed 18 other ignitions. Clearly fire policy was sound, but implementation was not at all uniform among the different agencies.

3. There are risks inherent in trying to manage fire, but they can be reduced by careful planning and preparation. Use of planned burning and other efforts to reduce hazard fuels near high value structures and to create fuel breaks along boundaries help reduce risks from both prescribed natural fires and wildfires.

In 1986, the National Fire Protection Association initiated a nationwide campaign to make people aware of the potential fire problem in what is called the urban/wildland interface, where builders have inadvertently created a fire hazard by trying to make human structures looks more "natural" with wood roofs and siding. Ironically, the 1988 fires in and around Yellowstone provided some textbook examples of why this kind of design can present problems: buildings were surrounded by forest fuels, "shake" roofs turned into firetraps, and nearby propane tanks turned into potential firebombs. Firefighters scurried around, cutting trees near buildings and picking up sticks to reduce the fuel load in park villages; instead of what should have been a planned, aesthetically sensitive effort done over a number of years, the tree cutting was, of necessity, done in a couple of days by fire crews.

It is interesting to note that although one of the objectives of the Yellowstone Park fire management plan is to allow all fires to burn, except when they threaten life and property, the plan says nothing about fire hazard reduction around buildings. The 1988 fires threatened almost every major facility in the park; the costs of protecting these facilities were extremely high because of the complete lack of fuel management in and around the structures. At times, fire crews were pulled off other wildfires and sent miles away to help defend the higher priority facilities.

4. The ecological effects of PNF support resource objectives, but the social and economic effects may be unacceptable in some cases. PNFs may affect permitted uses of parks and wilderness, such as recreation, and impact outside areas through such phenomena as smoke and stream sedimentation.

The fire policy review team found that because natural fires generally burn during the summer, they can have considerable impact on recreation. Although the various agencies' fire management plans did address these concerns, there were no specific criteria that could be used to address them in decisions about prescribed fires and wild fires. For example, there are no criteria that evaluate the possible recreational values that could be lost

under various prescribed fire alternatives; impacts could include damage to trails, trailhead facilities and outfitter camps. The fire management plans did little to consider the social and economic impacts outside the boundaries of the park or wilderness.

5. Dissemination of information before and during PNFs needs to be improved. There should be more public participation in the development of fire management plans.

The review team noted that there was little uniform, consistent and adequate information on either the location of fires or planned fire management actions, or on their implications for the public. Road closures in Yellowstone were erratic, frustrating both visitors and local residents. The main message was that these fires were the best thing that had ever happened to the Yellowstone area; meanwhile, the agencies involved were spending more than a million dollars a day fighting wildfires, which are unwanted events.

The 1988 fire season revealed the risk inherent in the management of PNFs, including high suppression costs and unacceptable social, environmental and natural resource impacts. The possibility of these risks were not addressed in the public review of fire management plans; people were therefore unaware of what could happen during major fire events. Thus, although the extreme weather and conditions of 1988 produced almost unstoppable fire behavior, the public held fire managers accountable for situations well beyond their control.

6. Internal management processes, such as training more personnel, developing uniform terminology and utilizing similar budget structures, would significantly improve fire management.

One particularly interesting finding was that Yellowstone Park officials were often only "paper trained": they had taken fire management training courses but lacked actual fire experience along the various levels of command and responsibility. This is a significant problem among fire managers in general, particularly when dealing with infrequent, high-intensity fires. Many agencies cope with the training problem by allowing personnel to participate on regional or national fire management teams. Unfortunately, most National Park fire managers have "co-lateral" duties: they may carry the title "fire management officer," but they are often also responsible for a number of other duties such as visitor safety.

Differing budget structures for fire management also affected the response to the 1988 fires. In 1988, all of the federal wildland management agencies, except the National Park Service, had to manage prescribed fires with budgeted dollars because it is considered a form of resource management, not an emergency event. Wildfires, on the other hand, are paid for by emergency fire suppression funds, an after-the-fact congressional appropriation. Congressional scrutiny has made decisions about designating fire as prescribed or wild quite important, and so most of these federal agencies have a very clear and defensible decision process. On the other hand, PNFs in National Parks, prior to 1988, were all paid for by after-the-fact congressional allocation, and, as a result, many Park Service fire management plans lack prescription criteria and clear-cut decision making processes.

7. Claims were heard that some managers support "naturalness" above all else, allowing fires to burn outside of prescription requirements without appropriate suppression actions.

The review team heard allegations from some fire management professionals, landowners and state forestry officials that some managers had intentionally allowed fires to burn beyond prescription limits or failed to take the appropriate suppression actions required for wildfires. Fires were allowed to burn freely, the allegations continued, as long as they stayed within the boundaries of a park or wilderness. Many of these allegations were not supported in the draft reviews of individual fires in the Greater Yellowstone Area.

The real fire effect of the 1988 Yellowstone fires was to severely set back PNF programs in the United States, Canada and Australia. The United States fire managers are perceived to be at the forefront of planning preparation and coordination. The Yellowstone events have reaffirmed Park Canada's prescribed burning program where only managers ignited fires and all lightning ignitions are suppressed. In Australia, it appears that plans for PNF programs may be discarded altogether. In the United States, at this time, only three National Parks have approved PNF programs out of 26 pre-1988 programs. Only 16 (5 million acres) U.S. Forest Service PNF programs have been approved out of the 50 (14 million acres) pre-1988 programs.

TABLE 1. Greater Yellowstone Area fire occurrence in 1988.

Unit	Acreage			Total	Initial Classification	
	0-1	1.1-10	10+		Prescribed	Wildfire
Beaverhead NF	3	0	3	6	0	6
Bridger-Teton NF	22	7	5	34	1*	33
Custer NF	9	0	2	11	1**	10
Gallatin NF	43	6	2	51	0	51
Grand Teton NP	15	2	2	19	1	18
Shoshone NF	15	1	5	21	0	21
Targhee NF	47	6	4	57	0	57
Yellowstone NP	24	2	24	50	28***	22
Totals	178	24	47	249	31	218

* Mink Fire: Started 7/11 and declared a wildfire 7/14
** Storm Creek Fire: Started 6/14 and declared a wildfire 7/3
***Twelve fires burned out at less than 1 acre and the rest became wildfires

Source: Greater Yellowstone Area Fire Situation 1988 report to the Greater Yellowstone Coordinating Committee, 1989.

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Early Development of Vegetation Following Holocaustic Fire in Northern Rocky Mountain Forests[1]

Introduction

Information about the recovery process and postfire development of forest vegetation has evolved from forest succession studies conducted in central and northern Idaho and western Montana. Permanent plots were sampled for species abundance annually for periods of 7 to 22 years. More than 60 study sites were involved. A study of the initial postfire communities establishing after the 1988 Northern Rocky Mountain holocaustic fires (including the Northfork Fire in Yellowstone National Park) indicates that the mechanism for initiating recovery and succession is the same as that displayed by the permanent plot succession studies.

Holocaustic Fire Treatment

Fire is an inherent phenomenon of Northern Rocky Mountain forests and has been the principal and most extensive initiator of forest succession in the region for at least the last several thousand years (Hemphill 1983, Mehringer *et al.* 1977, Wellner 1970). The severity of burning in these forests varies from light ground fires to severe, tree-overstory-killing crown fires (Arno 1980, Wellner 1970). Holocaustic fires (Stickney 1986) represents the severest natural burning disturbance sustained by Northern Rocky Mountain forest vegetation, and as such it provides the conditions to best assess the maximal limit of the ability of forest species to survive fire. A holocaustic fire is defined as one that incinerates all of the finer fuels on a site. Its characteristics in Northern Rocky Mountain forests are (1) destruction of the coniferous tree overstory, (2) reduction of the tree-shrub understory and herb layers to ground level, and (3) conversion of the dead organic mantle of the forest floor to ash down to the mineral ground surface. Although this fire treatment incinerates the above-ground portion of the forest community, the below-ground portion can remain intact and essentially undisturbed.

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-23, 1990, Corvallis, Oregon, Mark V. Wilson and Nan C. Vance, editors.

Initial Community Components

As defined by their postfire or seral origin (Stickney 1986), plants that compose the initial community establishing on burned sites after a holocaustic fire belong to one of three components: survivor, residual colonizer, and offsite colonizer. Survivors derive from burned plants capable of regrowth. Colonizers are postfire plants established from seed. Residual colonizers originate from burned sources. Offsite colonizers originate from sources not subjected to burning.

The Danish ecologist C. Raunkiaer classified plant life forms according to the position of their active growing points in relation to their exposure to air temperature of the "unfavorable season" (Raunkiaer 1934). The closer the growing points were to the ground the greater the capability to survive unfavorable temperatures. The survival mechanisms of Northern Rocky Mountain forest plants to fire may be visualized by applying Raunkiaer's idea to the position of both the dormant and active growing points exposed to the lethal temperatures of a holocaustic fire. This application shows that the coniferous tree (leftmost mode in Figure 1) has no mechanism by which to survive holocaustic fire treatment. Forest herb and shrub species with root crown or underground stem life forms are capable of surviving this kind of fire (Table 1, Figure 1). Thus, survivors of holocaustic fires are preburn plants with growing points near, in, or below the mineral ground surface.

Residual colonizers, whose seed was present on the site prior to the time of the fire, represent the other onsite source for species in the initial community. The seeds of residual colonizers survive fire treatment either in cones within tree crowns or as ground-stored seed (Figure 2). Residual colonizer seeds stored for a year or more in the ground characteristically exhibit poor dispersal capability, hard seed coat, and long-term viability. Although the number of species in this group constitute a small percentage of the seral flora, they represent some of the most abundant cover species

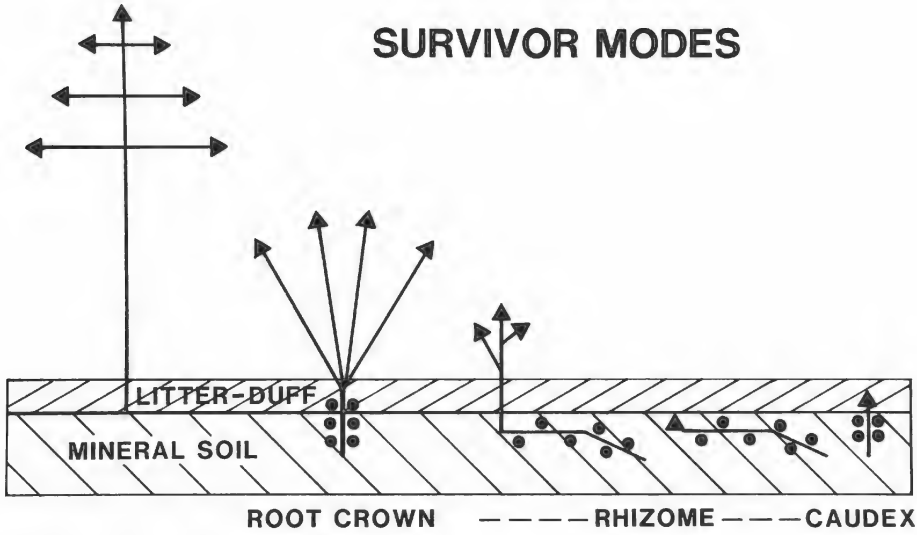

Figure 1. Raunkiaer's life forms modified to illustrate mechanisms that enable Northern Rocky Mountain forest plants to survive holocaustic forest fire. Triangles and dots represent active and dormant growing points respectively. The region from the forest canopy down to at least the mineral soil surface is subject to lethal temperatures from holocaustic fire. Active growing points within this zone are killed; protected dormant growing points are not.

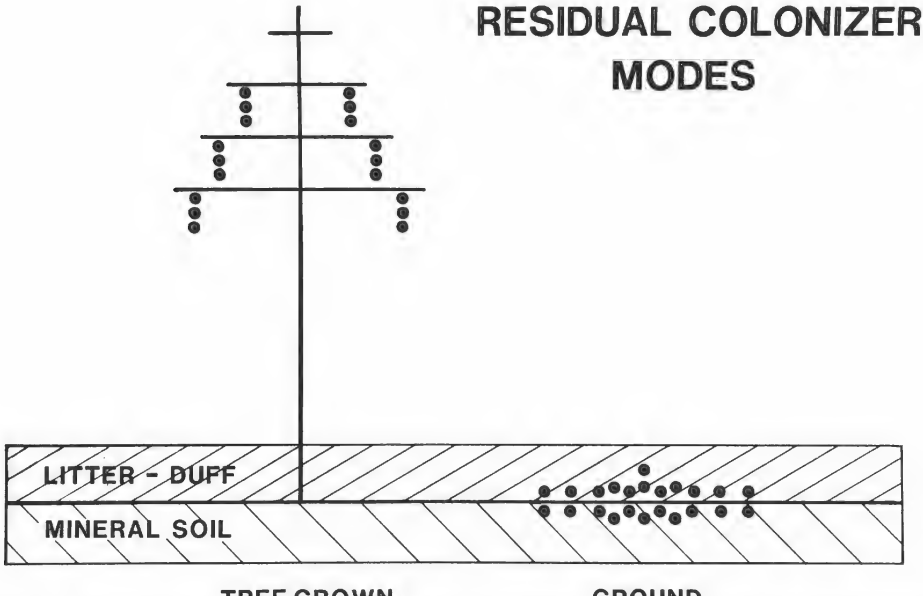

Figure 2. Location of dormant growing points for residual colonizers (dots represent viable seeds). Seeds situated from the top of the tree overstory down to the mineral ground surface are subject to lethal temperatures from holocaustic fire. Seeds in tree crowns are protected by cones; seeds in fruit in the canopy of other plants are not protected. Survival of seeds situated in the litter-duff layer depends on the characteristics of the seed coat. Seeds within the ground receive greater protection from the mineral substrate.

TABLE 1. Life forms and species from Northern Rocky Mountain forests that have demonstrated survival capabilities following holocaustic wildfires.

Life form	Species examples
Root crown shrub	*Acer glabrum, Alnus sinuata*
Rhizomatous shrub	*Spiraea betulifolia, Vaccinium globulare*
Rhizomatous herb	
Forb	*Arnica latifolia, Aster conspicuus*
Grass	*Calamagrostis rubescens*
Caudex herb	*Lupinus argenteus*
Deep-seated stem herb	*Erythronium grandiflorum, Trillium ovatum*
Rhizome-like root herb	*Epilobium angustifolium*

in the pretree stages of succession (Stickney 1986). Prominent examples of residual colonizers include the shrubs snowbrush (*Ceanothus velutinus*) and redstem (*C. sanguineus*); the herbs geranium (*Geranium bicknellii*), dragonhead (*Dracocephalum parviflorum*), and wild hollyhocks (*Iliamna rivularis*); and western larch (*Larix occidentalis*) and lodgepole pine (*Pinus contorta*).

Offsite colonizers are derived from seed originating from unburned sites usually outside the fire. Seeds of species characterizing this group of the initial community typically are small, light weight, and air dispersible with short-term viability. The number of species constituting the offsite component typically is large (including numerous members of the composite family) and greater than that for the residual colonizer component. Usually, a relative few become important cover species in the subsequent succession. Two of the more important offsite colonizers successionally in the Northern Rocky Mountains are the herb fireweed (*Epilobium angustifolium*) and the shrub Scouler's willow (*Salix scouleriana*).

Initial Community

Floristic composition of the initial community, the group of species that initiates the course of succession, derives from onsite (burned) and offsite (unburned) sources (Lyon and Stickney 1976, Stickney 1985). The interaction of the fire and onsite sources determines their presence in the initial community. The floristic contributions to succession from onsite sources, i.e., survivors and colonizers, are limited to those species present in the preburn forest (including its seedbank). The survivor component results from the effect of fire severity on prefire species composition. Generally, the more severe the burning treatment the higher the mortality and the less the survivor component in both species and plants. A sparse survivor component can also result from forests with little or no undergrowth vegetation that serves as a source for survivors. Similarly, the extent of a residual colonizer component is dependent on the seed already "in place" on the site. The contribution of plant species from onsite sources to the seral flora is a singular event in the succession cycle. On the basis of our permanent plot studies this event manifests itself, almost exclusively, in the first postfire year of succession.

Further additions to the floristic composition must come from offsite colonization. Unlike the onsite components, the potential for offsite species contributions to the initial community is limited only to the extent of the available flora. Species from offsite sources require no capacity to survive fire. Rather, in contrast to onsite species, they do require both a seed crop and a dispersal event that coincides with the availability of a burned site.

Thus, the floristic composition of the initial community established by the species of the survivor component and the residual and offsite colonizer components set the course of succession. Changes in the seral flora result only from the loss of initial community species (local extinction) or the addition of species from offsite colonization. Our permanent plot studies reveal that offsite colonization occurs but for a majority of sites does not alter the course of successional development established by the initial community (Stickney 1986). For those few cases where secondary colonization has had a significant influence on the course of succession, it was from postfire onsite rather than offsite seed sources.

Seral Spectrum

Various combinations of floristic composition and species abundance of survivor and colonizer species give rise to a spectrum of initial communities. Thus, the course or pattern of early forest succession for a given site can range from a survivor-dominated to a colonizer-dominated process. Brushfields occupying forest sites at the time of burning provide one example of a survivor-dominated succession. At Sundance Burn Study Site 17 the initial community consisted of survivor *Salix scouleriana, Ceanothus sanguineus,* and six

other species of shrubs, and the herbs pinegrass (*Calamagrostis rubescens*) and lupine (*Lupinus argenteus*) (Stickney 1985). All these species regrew profusely following a holocaustic wildfire. Recovery was rapid, and 20 years later survivor-origin *Salix*, *Ceanothus*, and *Calamagrostis* were still the most abundant species and made up most of the vegetation.

Illustrative of the other end of the spectrum is Miller Creek Study Site 22 where the forest overstory was killed and shrubs and herbs subjected to high mortality (Stickney 1980). The resulting small survivor component, with its slow recovery rate, provided a highly favorable site for the establishment of colonizers. In this instance large populations of both offsite (*Epilobium angustifolium*) and residual (*Ceanothus velutinus*, *Pinus contorta*, and *Larix occidentalis*) colonizers became established in succession year 1. Rapid development of *Epilobium* dominated the herb stage through year 6. This was followed by a shrub stage in which the development of seedling *Ceanothus* constituted the predominant shrub to year 20 and beyond. Concomitant with the establishment of *Ceanothus* seedlings were seedlings of *Pinus* and *Larix* trees. Their height growth was such that they overtopped the shrub canopy by the beginning of the shrub stage. As shrub coverage, principally *Ceanothus*, increased, *Epilobium* declined. By the 20th year the beginning of the decline of *Ceanothus* was associated with the continual development of the tree canopy. All the prominent colonizer species thus far constituting the succession were present in the initial community. After 20 years of recovery and development, secondary colonization from offsite sources has yet to make an influential contribution. With further development of tree overstory canopy, the recovering survivor understory species should again constitute a prominent element of this forest vegetation.

In 1989 a study of the fires of 1988 in the Northern Rocky Mountains revealed the same spectrum of initial communities found in the permanent plot successional studies. Examples illustrating predominant survivor component (*Calamagrostis rubescens*, aster (*Aster conspicuus*)) and residual colonizer component (*Dracocephalum parviflorum*, *Geranium bicknellii*) were observed within the Northfork Burn in Yellowstone National Park. The occurrence of these types of initial communities suggests that recovery and seral development of these burned forest communities should follow patterns similar to those documented elsewhere in the Northern Rockies.

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Biological Effects of Petroleum Hydrocarbons: Predictions of Long-term Effects and Recovery[1]

Biological effects of petroleum hydrocarbons on marine organisms and ecosystems are dependent on the persistence and bioavailability of specific hydrocarbons, the ability of organisms to accumulate and metabolize various hydrocarbons, the fate of metabolized products, and the interference of specific hydrocarbons with normal metabolic processes that may alter an organism's chances for survival and reproduction in the environment. The responses of organisms to petroleum hydrocarbons can be manifested at four levels of biological organization: (1) biochemical and cellular; (2) organismal, including the integration of physiological, biochemical and behavioral responses; (3) population, including alterations in population dynamics; and (4) community, resulting in alterations in community structure and dynamics (Table 1). Impairment of behavioral, developmental and physiological processes may occur at concentrations significantly lower than acutely toxic levels; such responses may alter the long-term survival of affected populations. Thus, the integration of physiological and behavioral disturbances may result in alterations at the population and community levels (Capuzzo, 1987).

Populations of plaice *Pleuronectes platessa* collected from oil-contaminated estuaries following a spill from the *Amoco Cadiz* exhibited reduced growth rates and fecundity in addition to histopathological aberrations (Conan, 1982). Krebs and Burns (1977) studied populations of the fiddler crab *Uca pugnax* for seven years after a spill of No. 2 fuel oil from the barge *Florida.* They observed long-term reductions in recruitment, population density, female:male ratios of adult crabs, behavioral changes and high overwintering mortality. Recovery of crab populations was correlated with the disappearance of naphthalenes and alkylated naphthalenes from contaminated sediments. Similar patterns of long-term changes in recruitment and density of benthic fauna have been observed with other oil spills (Gilfillan and Vandermeulen, 1978; Thomas, 1978; Cabioch *et al.*, 1980; Sanders *et al.*, 1980; Beslier *et al.*, 1980; Glemarec and Hussenot, 1981; Elmgren *et al.*, 1983). Mesocosm experiments have further documented that major long-term changes in marine ecosystems from oil spills occur in the benthos (Grassle *et al.*, 1981; Oviatt *et al.*, 1982).

In considering the long-term effects of petroleum hydrocarbons on marine ecosystems it is important to ascertain what biological effects may result in subtle ecological changes, changes in community structure and function, and possible impairment of fisheries resources. Sublethal effects of petroleum hydrocarbons at the organismal and population levels include impairment of feeding, growth, development, energetics and recruitment, alterations in reproductive and developmental potential of populations, and possible changes in population structure and dynamics. It is difficult, however, to relate chronic responses of organisms to petroleum hydrocarbons to higher level alterations in the functioning of marine ecosystems or in the sustainable yield of harvestable fisheries resources. Although a wide range of sublethal stress indices have been proposed for evaluation of chronic responses of organisms to petroleum hydrocarbons, few have been linked to the survival potential of the individual organism or the reproductive potential of the population. The sensitivity of early developmental stages, the impairment of reproductive processes, and the long-term effects on populations suggest that chronic exposure to petroleum hydrocarbons may certainly alter the dynamics of benthic populations, including populations of valuable commercial resources.

In assessing long-term impact of petroleum contamination, it is important to understand the conditions under which hydrocarbons persist in benthic environments and the sublethal effects that lead to reduced growth, delayed development and reduced reproductive effort, population decline and the loss of that population's function in marine communities. Such a task requires an understanding of: (1) the physical processes (specifically flow characteristics) that influence the partitioning of contaminants between sediments and water; (2) the

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-23, 1990, Corvallis, Oregon, Mark V. Wilson and Nan C. Vance, editors.

TABLE 1. Response levels of marine organisms to petroleum hydrocarbons

Level	Types of Responses	Effects at Next Level
Biochemical-Cellular	Toxication Metabolic impairment Cellular damage	Toxic metabolites Disruption in energetics and cellular processes
	Detoxication	Adaptation
Organismal	Physiological changes Behavioral changes Susceptibility to disease Reproductive effort Larval viability	Reduction in population performance
	Adjustment in rate functions Immune responses	Regulation and adaptation of populations
Population	Age/Size structure Recruitment Mortality Biomass	Effects on species productivity and coexisting species and community
	Adjustment of reproductive output and other demographic characteristics	Adaptation of population
Community	Species abundance Species distribution Biomass Trophic interactions	Replacement by more adaptive competitors Reduced secondary production
	Ecosystem adaptation	No change in community structure and function

chemical processes that influence contaminant availability, persistence, and degradation in sediments and water; and (3) the long-term biological effects that alter population stability and the consequences of such effects on resource utilization. The first two aspects are important in establishing realistic exposure scenarios—both in time and space—and the third is important in linking ecological effects with concerns of contamination of resources. Only through a multi-disciplinary approach to the study of the fate, transport and effects of petroleum hydrocarbons on marine ecosystems will there be a significant improvement in our ability to predict the long-term effects of oil spills and to elucidate the mechanisms of recovery.

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Regional Vertical Tectonic Displacement of Shorelines in South-central Alaska During and Between Great Earthquakes[1]

Introduction

The 1964 Alaska earthquake was the greatest seismotectonic event of the 20th century in its extent of tectonic deformation. The earthquake caused sudden changes in elevation along several thousand kilometers of shoreline over an area equal to about 2/3 that of California with corresponding instantaneous changes in the habitat of the shoreline biota.

This paper briefly reviews the setting of the 1964 earthquake and the unprecedented tectonic deformation that accompanied it. The paper outlines research directed towards defining the deformation that occurs between great earthquakes (interseismic part of the seismic cycle) and the long-term history of deformation over repeated seismic cycles in the earthquake-affected region, emphasizing work in progress. An understanding of this record of deformation is basic for evaluating how frequently 1964-type events recur in this same region, for improved understanding of the earthquake cycle in great subduction-zone seismotectonic events, and for predicting future great earthquakes in this and tectonically similar regions elsewhere.

As used in this paper, "strandline" refers to the extreme high tide shoreline, "emergence" and "submergence" refer to the vertical displacement of strandlines relative to sea level, "uplift" and "subsidence" refer to episodic tectonic and gradual isostatic vertical displacements of strandlines, "marine terrace" refers to a surf-cut or constructional platform that slopes gently seaward from the strandline and is backed by a sea cliff on the landward side, and "eustatic sea level" refers to the worldwide long-term rise and fall of sea level. The long-term submergence rate (averaged over several earthquake cycles) includes a eustatic sea level rise of about 0.75 mm/yr during the past 5,000 years (Bard et al., 1990) and a possible apparent sea level rise in this region due to gradual isostatic subsidence of about 0.5 mm/yr (Peltier and Tushingham, 1989).

1964 (Coseismic) Deformation

The 1964 Alaskan earthquake involved a segment of the eastern Aleutian arc 800 km long (Fig. 1). This major tectonic event was characterized by: (1) shallow seismicity (<30 km), with most of the earthquakes located between the Aleutian trench and the zero isobase (the area between the zones of major uplift and subsidence); (2) regional vertical displacements in a broad asymmetric downwarp to 2 m centered over the Kodiak, Kenai, and Chugach Mountains with flanking zones of marked uplift to 11.3 m on the seaward side and minor uplift to about 0.3 m on the landward side that extends north of the Alaska Range; and (3) geodetically-measured horizontal displacements that involved systematic shifts of the land in a generally seaward direction of at least 20 m in the region between Anchorage and Montague Island (Plafker, 1969; 1972). More than 140,000 km^2 experienced major vertical deformation. The Patton Bay and Hanning Bay faults, subordinate northwest-dipping reverse faults, displaced the surface on Montague Island. The Patton Bay fault, with at least 7.9 m dip-slip, extended offshore to the southwest onto the continental shelf.

Regional vertical displacements, both upward and downward, caused profound modifications in shoreline morphology and attendant widespread effects on the biota. Changes in the position of shorelines relative to sea level directly affected numerous coastal installations, shipping, and the fishing and shellfish industries. A major indirect effect of the sudden uplift of the sea floor was generation of a train of sea waves (tsunami) that were responsible for 35 of the 115 fatalities and for much of the property damage attributable to the earthquake both in Alaska and all along the coast of the Pacific northwest as far away as central California (Plafker, 1969).

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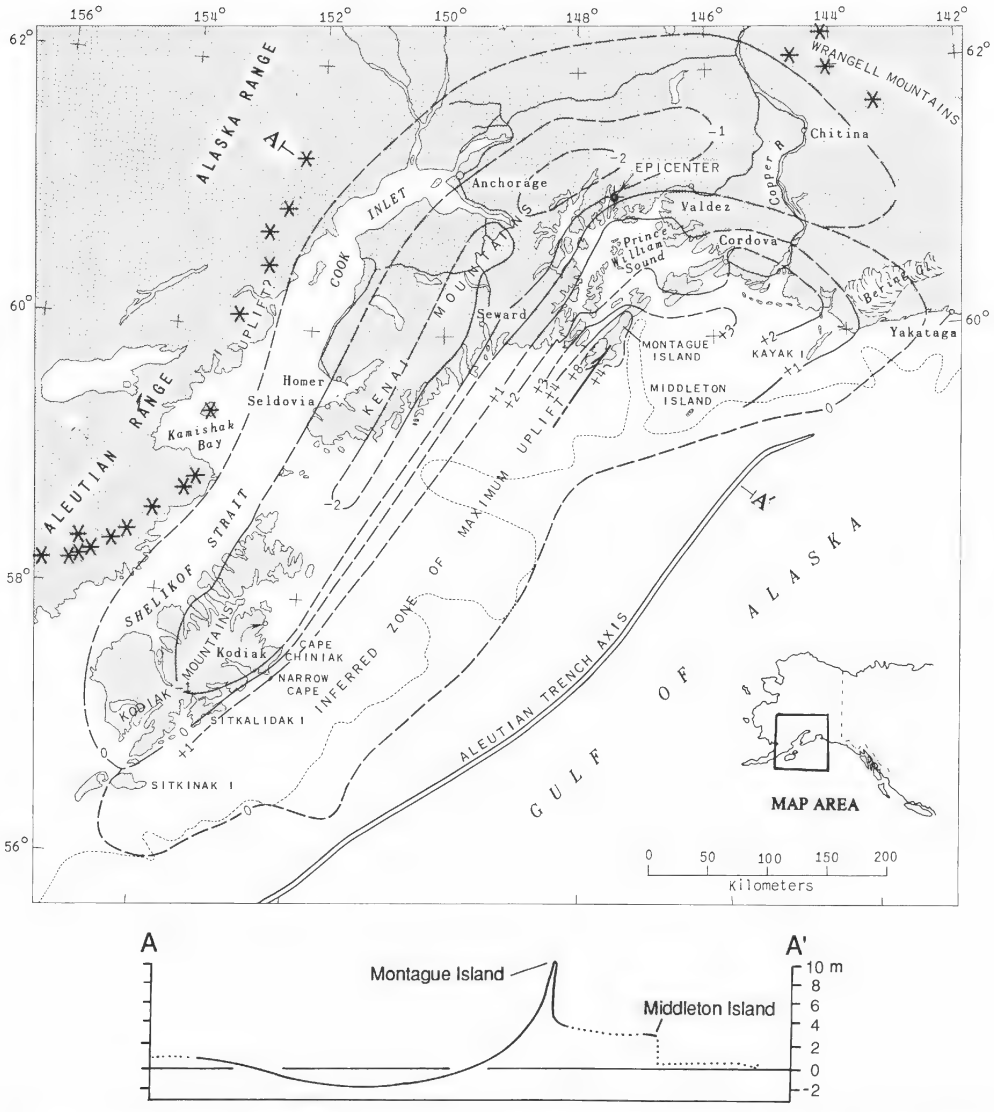

Figure 1. Tectonic uplift and subsidence that accompanied the 1964 Alaska earthquake. The land-level change, in meters, is shown by the contours, which are dashed where approximate or inferred. The outer edge of the continental shelf, at −200 m, is indicated by a dotted line, the Aleutian Trench axis is shown by a double solid line, and active or dormant volcanoes of the magmatic arc are shown by stars. The profile below shows coseismic vertical displacements along line A-A'. After Plafker (1969).

Paleoseismic Data

Records of historic earthquakes, especially in North America, do not span even one full cycle of recurrence of magnitude 8 earthquakes at any given site. The recurrence interval, or duration of time between 1964-type seismotectonic events can be deduced from paleoseismologic studies of shorelines that have undergone repeated coseismic uplift or submergence. The techniques of paleoseismology

are primarily geologic (Wallace, 1981); in the area affected by the 1964 Alaska earthquake, paleoseismologic data on previous great seismotectonic events comes from radiocarbon dating of shoreline deposits that experienced both sudden coseismic uplift and subsidence. The extensive coastline affected by vertical displacements provided a unique opportunity to determine not only the coseismic displacements, but the longer-term history of displacements relative to sea level. Much of the earthquake-affected region has also been subject to variable amounts of interseismic tectonic subsidence that greatly exceeds the eustatic sea level rise. Therefore, it is the combination of the coseismic, post-seismic, and interseismic displacements that, together with eustatic sea level change and isostatic movements, determine whether a particular strandline will exhibit net uplift, net subsidence, or stability relative to sea level over many earthquake cycles. Because of the short historic record of less than 250 years in Alaska and an even briefer instrumental record, geologic techniques provide the only means for deducing the long-term late Holocene record of vertical tectonic displacements in the region and recurrence intervals of great 1964-type events.

Areas of Pre-1964 Interseismic Submergence

Much of the region affected by both coseismic uplift and subsidence during the 1964 Alaskan earthquake is characterized by gradual interseismic shoreline submergence between earthquakes. Pre-1964 subsidence is documented by widespread drowning of coastal forests and fresh water peat deposits (Fig. 2) on the southeast coast of Kodiak Island, the Seldovia area of lower Cook Inlet, the Girdwood-Anchorage area of upper Cook Inlet, throughout Prince William Sound, along the front of the Copper River delta and along the mainland coast and Kayak Island between the Copper River delta and Bering Glacier (locations on Fig. 1).

Stratigraphic studies and radiocarbon dates of the shoreline deposits indicate that the pre-1964 submergence in Prince William Sound and at the Copper River delta represents at least 800 years at rates that range from about 5 to 8 mm/yr and average close to 7 mm/yr. The U. S. Geological Survey is currently using stratigraphy and radiocarbon ages of intertidal plant fossils to elucidate details of the interseismic subsidence history of the

Figure 2. Tree stumps rooted in peat exposed at low tide near the mouth of Pete Dahl Slough, Copper River Delta. These stumps and the associated peat are remnants of a widespread subaerial flora on the Copper River delta that was submerged 2-3 m below highest tides by tectonic subsidence prior to 1964 and buried by intertidal silt and mud deposited by distributaries of the Copper River. Similar remnants of submerged forests and subaerial peat are present throughout much of the Gulf of Alaska margin from Kodiak Island to Bering Glacier.

Copper River delta. Radiocarbon-dated samples from the drowned strandlines demonstrate that the pre-1964 submergence probably occurred gradually or in small increments over at least 800 years. The duration of this regional submergence provides an approximate measure of the time since the last major 1964-type tectonic earthquake in the same region.

Areas of Coseismic and Long-Term Emergence

Emergent Holocene terrace sequences in the Gulf of Alaska region formed as a series of upward pulses that were separated by intervals of stability or even gradual submergence. These upward pulses presumably represent earthquake-related movements similar to the emergence that affected the same coasts during the 1964 event.

The most complete and best-studied record of successive uplifts in the area affected by the 1964 Alaska earthquake is preserved in a steplike flight of marine terraces at Middleton Island, 80 km off the mainland coast near the edge of the continental shelf (Plafker, 1969, 1986; Plafker and Rubin, 1978). Pulsating emergence of the island is recorded by six gently-sloping wave-cut marine terraces that are separated by seacliffs or rises (Fig. 3). Average strandline elevations are about 3.5, 11, 20, 26, 36, and 46 m; the 3.5-m terrace was

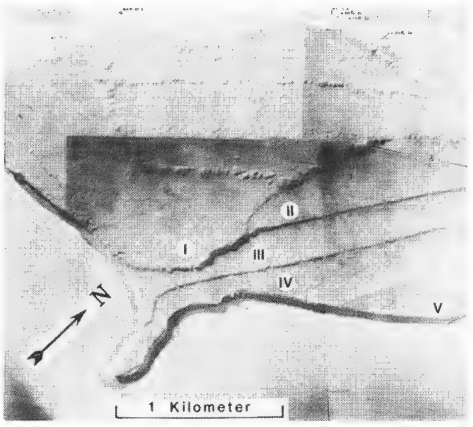

Figure 3. 1947 vertical aerial photo mosaic of the southeastern end of Middleton Island showing benches and seacliffs of the five pre-1964 marine terraces that were formed by 5-7 m coseismic uplift steps since emergence of the island about 4,900 years ago (see Figure 4 for elevations and ages). Terraces are identified by Roman numerals which correspond with those shown in Figure 4.

uplifted suddenly during the 1964 earthquake. Radiocarbon ages (all ± approximately 140 years) have been determined for the five pre-1964 terraces (Plafker and Rubin, 1978, Table 1). A plot of terrace ages vs elevation (Fig. 4) shows that (1) the last previous uplift was about 1,300 years ago; (2) sudden uplifts have occurred at Middleton Island at intervals of about 400 to 1,300 years (average 800 years) since the island emerged from the sea about 5,000 years ago; and (3) the average rate of emergence is about 9 mm/yr, but only about 5.8 mm/yr during the past 1,300 years. If the deformation rate is constant, the patterns from the dated terraces on Middleton Island indicate that another tectonic earthquake involving uplift of the island is overdue. Many more data of this kind are needed, however, before prediction, even on a time scale of centuries, becomes practicable. Nevertheless, the Middleton Island data demonstrate the potential of relatively inexpensive geomorphic studies for significantly extending the historic record of tectonic earthquakes in coastal regions.

Areas of Coseismic Uplift and Long-Term Stability

Some coastal areas affected by coseismic uplift may also experience gradual interseismic subsidence that equals or exceeds the coseismic displacement. For example, at Montague Island interseismic tectonic subsidence plus eustatic sea level rise is almost equal to large increments of coseismic uplift (9-11 m in 1964) so that strandline elevations show less than a meter of net change over a period of about 4,500 years.

Areas of Coseismic Uplift and Long-Term Submergence

The Copper River delta area east of Cordova has an exceptionally complete record of multiple coseismic uplift events separated by gradual interseismic submergence that exceeds the coseismic uplift, which was about 2 m in the 1964 earthquake. Fresh water peat, brush, and trees cover the subaerial part of the delta and salt marsh, mainly *Carex/Potentilla* community type, occupies broad upper tidal flats (Thilenius, this volume). The stratigraphic record contains multiple fresh water peat and forest layers interbedded with intertidal silt and mud containing salt marsh plants (Figs. 5-9). This record indicates that interseismic submergence (tectonic subsidence plus eustatic sea level rise) exceeds coseismic uplift resulting in net submergence of the delta. Because of the high sedimentation rate on the delta (Reimnitz, 1966), accumulation of intertidal silt and mud keeps pace with submergence over much of the delta and the successive uplift events are recorded in the stratigraphic section as peat and forest horizons buried beneath layers of intertidal sediment (Figs. 5-9). Preliminary data from radiocarbon-dated samples of buried subaerial peat and wood indicate that the process has been continuous for at least 3,500 years, during which there were at least four pre-1964 coseismic uplift events of 2-3 m each. Figure 10 shows the stratigraphic section and a plot of age versus depth for the upper two subaerially-exposed pre-1964 events (Figs. 5-8). Recurrence intervals for the last two earthquakes are about 780 ± 115 and 670 ± 180 years; preliminary data from auger drill samples (not shown on Fig. 10) suggest at least two additional older events with recurrence intervals of about 800 and 650 years. The amount of coseismic uplift in the pre-1964 events is comparable to that which accompanied the 1964 earthquake suggesting that they were probably formed during earthquakes of comparable magnitude and type.

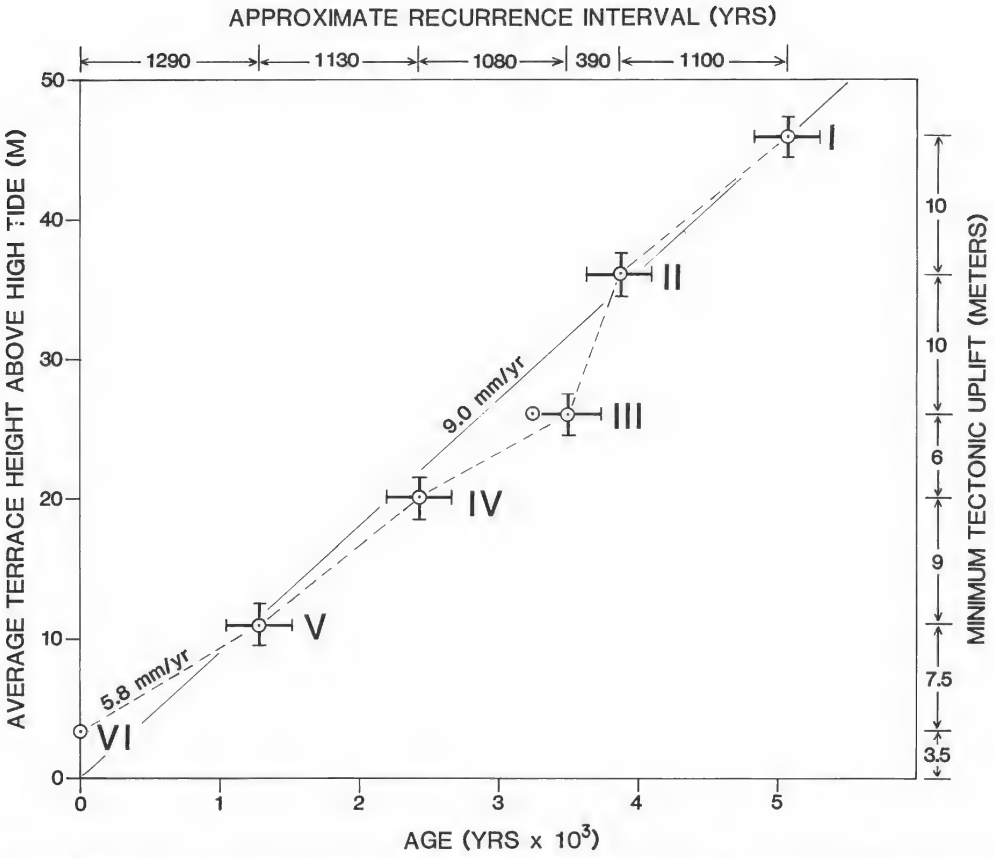

Figure 4. Ages and elevations of marine terraces at Middleton Island known or inferred to have been formed by earthquake-related uplift (see Figure 1 for location). The inferred recurrence intervals in calibrated radiocarbon years are shown at the top of the graph, and the approximate tectonic uplift per event is shown on the right side of the graph. Uplifts shown do not include the eustatic sea level rise of about 0.75 mm/yr during time interval shown. Terraces are identified by Roman numerals with the 1964 coseismic uplift of about 3.5 m at zero years (terrace VI). Solid line indicates long-term average pre-1964 uplift rate and dashed lines indicate average uplift rate between terraces. Note the discrepancy between the long-term uplift rate (9 mm/yr) and the change in rate since formation of terrace V (about 5.8 mm/yr). After Plafker (1987).

Areas of Coseismic Subsidence

Evidence for prehistoric earthquake-related displacements in regions affected by coseismic subsidence in protected localities may be even better than in areas of uplift, because readily identifiable soil, peat, and forest horizons tend to be buried and preserved beneath transgressive intertidal deposits. At least two such buried soil and forest horizons are well exposed in the intertidal zone at Girdwood in upper Cook Inlet in an area where there was 1.5-2 m coseismic subsidence in 1964 (Fig. 1). The upper horizon at Girdwood, at a pre-1964 depth of about 0.7 m is at least 700 years old, and the lower horizon, at about 4.5 m depth is about 2,800 years old (Karlstrom *In* Plafker, 1969, Table 5). At this locality, submergence of the upper horizon, and much of the submergence of the lower horizon could be attributable to the eustatic sea level rise. On-going studies of intertidal and subsurface sections in the upper Cook Inlet region have identified at least 7 submerged organic layers as much as 4,500 years old and to a depth of more than 12 m (Bartsch-Winkler and Schmoll, 1987; Combellick, 1986). Because of limited exposures of intertidal layers and the difficulty of interpreting subsurface

Figure 5. Bank exposure in lower Alaganic Slough at locality depicted in Figure 10, showing resistant ledges formed by a lower bed of fresh-water peat 24 cm thick (foreground) and an upper bed of peat to 51 cm thick that locally contains rooted stumps of brush and small trees (background). The peat beds are enclosed by intertidal silt and mud which is typically varved due to annual variations between high summer and low winter discharge of the Copper River.

Figure 6. Close-up of the upper peat horizon in Figure 5 which contains abundant roots of small trees and brush. Before 1964 coseismic uplift of 2 m, high tides were above the brush that now grows at the top of the bank; the present highest tides are about 1.5 m above the upper peat horizon. Brush at the top of the bank postdates the 1964 uplift.

samples, it is not clear how many of these dated organic layers are earthquake-related, but at least some of them probably formed in 1964-type events. On-going studies are aimed at distinguishing earthquake-related organic layers from those formed by other processes active in this region.

Conclusions

Data on tectonic displacements related to the March 27, 1964 Alaska earthquake and postseismic and paleoseismologic data from the same region demonstrate the complexity and tectonic mobility of the earth's crust at the eastern end of the Aleutian arc. As a result of the vertical coseismic displacements, extensive coastal areas were abruptly elevated above sea level or lowered below sea level with attendant cataclysmic effects on the near-shore flora and fauna and on the works of man. Similar abrupt changes have been known to accompany great arc-related earthquakes in other parts of the world and are certain to recur in the future.

Paleoseismic studies along the coast in the earthquake-affected region provide unique data on interseismic vertical displacements and the longer-term late Holocene vertical fluctuations. The paleoseismic data indicate the following: (1) a complex seismic cycle exists in which interseismic submergence may equal or exceed coseismic uplift; (2) at least 800 years have elapsed since the last 1964-type earthquake in this same region; and (3) recurrence intervals for great 1964-type events on the order of 600-850 years in the Copper River delta-Prince William Sound region, and 400-1,300 years in the Middleton Island-Icy Bay region. These data indicate that regional scale coseismic vertical displacements and gradual interseismic submergence that locally exceeds the eustatic sea level rise have characterized this part of the Aleutian arc for at least the past several thousand years. More precise radiometric dating of paleoshoreline deposits is required in order to work out the details of the Quaternary deformational processes. Improvements in our understanding of the earthquake cycle may eventually enable us to determine the relative susceptibility of specific localities along the coast to future tectonic movements such as those that accompanied the 1964 earthquake.

Figure 7. Close-up of lower peat showing typical abrupt basal contact over lighter-colored varved intertidal silt and mud containing *Carex*. This contact is interpreted as a sudden uplift event that brought the area above the intertidal zone. It is comparable to the approximately 2-m uplift that accompanied the 1964 earthquake in this area. The abrupt upper contact of the peat marks the marine transgression that killed the subaerial plant community after gradual interseismic subsidence lowered it below extreme high tide. Radiocarbon ages of the base and top of the peat indicate that the duration of subaerial conditions at this site was about 200 years.

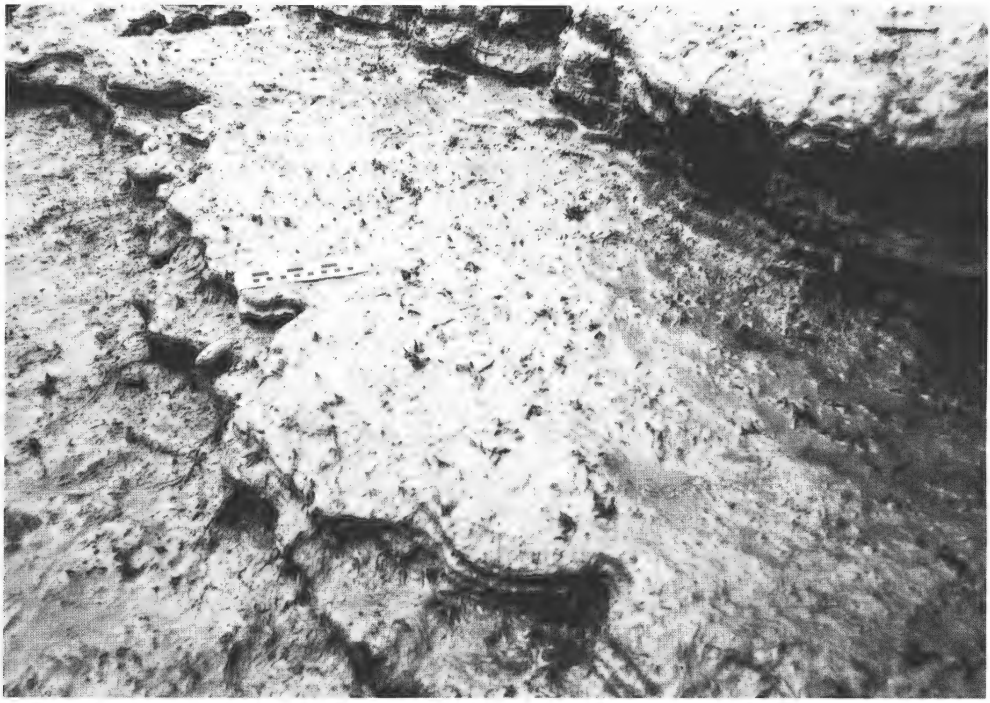

Figure 8. Varved intertidal deposits of silt and mud containing abundant fossil high salt marsh plant remains in growth position (mainly *Caryx lyngbei*). The continuous accumulation of lithologically uniform, varved, intertidal silt and mud between peat layers suggests gradual and largely uninterrupted interseismic subsidence of the Copper River delta. Varve counts and radiocarbon ages of *Carex* fossils in these deposits suggest submergence rates of about 4-5 mm/yr (3.8-5.1 mm/yr tectonic subsidence, plus 0.75 mm/yr eustatic sea level rise). Scale graduations are in centimeters and inches.

Figure 9. Present extreme high tide shoreline at the mouth of Alaganic Slough showing marsh vegetation (mainly *Caryx lyngbei* and *Potentilla*) growing in intertidal silt and mud up to extreme high tide level and post-1964 brush and trees above the highest tides. The new peat and forest horizon is forming in a very low-relief coastal strip to 4 km wide that was uplifted about 2 m in 1964.

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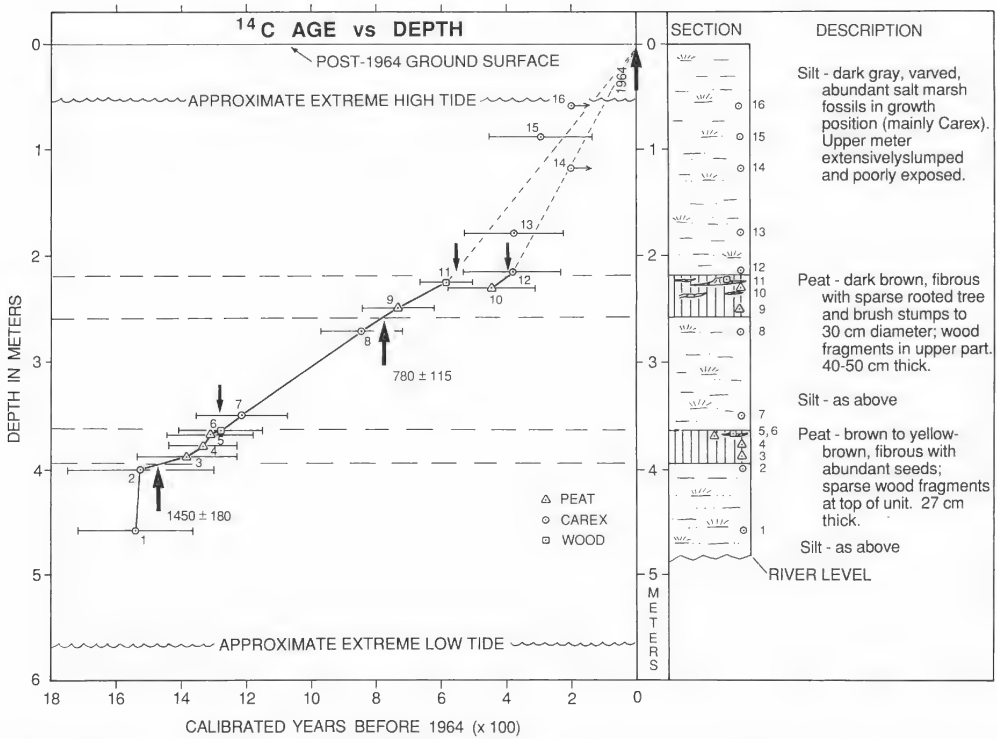
^{14}C AGE vs DEPTH
POST-1964 GROUND SURFACE
APPROXIMATE EXTREME HIGH TIDE
APPROXIMATE EXTREME LOW TIDE
780 ± 115
1450 ± 180
PEAT
CAREX
WOOD
SECTION
DESCRIPTION
Silt - dark gray, varved, abundant salt marsh fossils in growth position (mainly Carex). Upper meter extensivelyslumped and poorly exposed.
Peat - dark brown, fibrous with sparse rooted tree and brush stumps to 30 cm diameter; wood fragments in upper part. 40-50 cm thick.
Silt - as above
Peat - brown to yellow-brown, fibrous with abundant seeds; sparse wood fragments at top of unit. 27 cm thick.
Silt - as above
RIVER LEVEL
DEPTH IN METERS
METERS
CALIBRATED YEARS BEFORE 1964 (x 100)

Figure 10. Stratigraphic section exposed at lower Alaganic Slough (Figs. 5-8) and plot of radiocarbon-dated samples vs. elevation for subaerial peat and wood and intertidal marsh plants in silt. The heavy arrows indicate inferred sudden earthquake-related uplift at this site with resulting change in the depositional environment from intertidal silt and mud to fresh water peat in 1964, and at about 780 and 1,450 (each ± 140) years ago. Smaller arrows indicate the inferred time at which the subaerial organic layer was submerged below high tide, with two options shown for the upper horizon. Lines connecting dated samples indicate the average submergence rate, with two options shown by dotted lines for submergence of the upper horizon.

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Plant Succession on Earthquake Uplifted Coastal Wetlands, Copper River Delta, Alaska[1]

Introduction

The delta formed by the Copper River, extending for more than 75 km along the coastline of south-central Alaska, supports the most extensive coastal wetland on the Pacific Coast of North America. All major rivers that flow into the delta rise either directly from glaciers or from large moraine lakes and carry extremely high loads of very finely textured, suspended sediments. The Copper River alone is estimated to deposit an average of 97 million metric tons of sediment a year into the Gulf of Alaska. The Copper River Delta has approximately 1000 km^2 of intertidal and supertidal wetlands and associated creeks, rivers, pond and lakes. Offshore barrier sand islands, subtidal estuary, floodplains, river terraces, recent glacier outwash piedmonts cover about the same area.

In 1964, an earthquake of Richter Magnitude 8.4 to 8.6 raised the entire delta 1.8-3.4 m above the previous mean sea level. The tidal regime was significantly altered: large areas of subtidal estuary became intertidal and much of the intertidal wetlands became supertidal. As a result, the rate and pattern of plant succession were also significantly altered.

Physiography and Tidal Regime of the Wetlands

Most of the intertidal wetland is a relatively featureless flat with an average surface slope of about 0.25%. The topography is broken by river and stream channels, levees and mound islands and ridges. The substrate is tightly packed glacial sediments. The predominant material is fine silt, but thin layers of fine sand are frequent near the edges of drainage channels. Supertidal wetlands with tidally deposited silt substrate presently extend 4-10 km inland from the estuary. Much of this supertidal zone was intertidal before the uplift. The inland edge is the seaward boundary of the outwash piedmonts of four glaciers that originate in the front range of the Chugach Mountains and flow directly into the Copper River Delta. At the boundary the slope of the land increases 0.5-1.6 m per kilometer and the substrate changes from silt to silt-sand-fine gravel.

The tidal cycle is wide ranging, varying from −1.1 m to 4.5 m. High water levels may exceed 4.0 m in any month, but the highest spring tides occur from November through January. A well defined tidal wedge is present in the estuary and major river channels. Saline surface water is present in the estuary 2-2.5 km seaward of the foreshore levee. Salinity is in the 20-25 parts per thousand range throughout the summer; in winter it may reach 32 parts per thousand. Tidal influence extends inland more than 10 km.

During May-October the water flooding the upper reaches of the present intertidal zone in the western part of the Copper River estuary is often fresh or minimally brackish. Throughout the growing period a continuous, large volume of freshwater flows directly into the estuary. Ocean water propelled by strong onshore winds penetrates farther inland into the estuary, river channels and wetland drainage system in winter. However, the living parts of dormant plants in these tideflats are buried in the substrate or covered by freshwater ice and snow and protected from direct contact with saltwater.

River sediment is least in winter when glaciers move and melt more slowly. Secchi transparencies of 1-2 m are present at the start of significant glacier melting, usually in early to mid June. At this time, Secchi transparencies can decrease to less than 10 cm within 24 hours. Rivers remain highly turbid until late fall. The water is high in transported sediments, but generally low in dissolved ions. Temperature of runoff water rarely exceeds 6° C, although water flowing from supertidal wetlands has temperatures of 20° C or more.

Present Wetland Vegetation

Gramnoids are much more common on the Copper River delta than forbs or shrubs. The most

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-33, 1990, Corvallis, Oregon, Mark V. Wilson and Nan C. Vance, editors.

ubiquitous and abundant plant is lyngbye sedge (*Carex lyngbyaei*). It grows throughout both intertidal and supertidal wetlands and usually is the most abundant taxon in the herbaceous stratum. On intertidal wetland in seaward locations it occurs as a virtual monoculture. Species richness on the intertidal wetland increases, as the potential frequency of tidal inundation decreases. Grasses bluejoint (*Calamagrostis canadensis*), red fescue (*Festuca rubra*) and hairgrass (*Deschampsia beringensis*)) are more abundant on supertidal levees and in interlevee basins. Silverweed (*Potentilla egedii*) is the most important forb on infrequently flooded intertidal levees. Wild flag (*Iris setosa*), water hemlock (*Cicuta douglasii*), horsetail (*Equisetum arvense*) and vetchling (*Lathyrus palustris*) are other abundant and widely distributed forbs, especially on supertidal wetland.

The low-shrub sweetgale (*Myrica gale* var. *tomentosa*) forms dense stands on levees and upper channel banks in the supertidal wetland. The roots of *Myrica gale* var. *tomentosa*, a nitrogen fixer, are heavily nodulated even in tidal habitats. It is better adapted to substrates with more or less permanent high water tables than the other major shrub taxa.

Shrub vegetation covers almost the entire outwash piedmont. In habitats where there is a permanent watertable at or near the substrate surface, willows (particularly barclay willow (*S. barclayi*)) and undergreen willow (*S. commutata*) form a closed-canopy, tall-shrub overstory stratum 2-4 m high. *Myrica gale* var. *tomentosa* forms a low shrub understory under the willow and occurs in pure low shrub stands. Sitka alder (*Alnus crispa* ssp. *crispa*) shrubland is present on well aerated gravelbars, river terraces and sandbars in braided river channels. Shrubby black cottonwood (*Populus balsamifera* ssp. *tricocarpa*) is present in most alder stands and often forms a well defined overstory tree stratum. *Alnus crispa* spp. *crispa* and *Populus balsamifera* ssp. *tricocarpa* are pioneer species on occasionally flooded, coarse textured substrates. The eventual development of the tree overstory is caused by the greater stature of these slower-growing species and not by their invasion into established vegetation.

Primary Succession by *Carex lyngbyaei* on Uplifted Estuarine Surfaces

The developmental pattern sequence of *Carex lyngbyaei* is single culms, tussocks, patches, separate rings, coalesced rings, linear clumps, to meadow. Initial establishment occurs first on the inside curves of the levees which parallel the channel. Eventually sedge occupies the levees on both sides of the channel. After forming into linear bands the sedge spreads outward into the slightly lower elevation interlevee basin. The ring pattern persists after the full tidal meadow develops. Peripheral culms are taller, more dense, and have a darker green color than the culms in the center. Surface accretion proceeds at a faster rate in the peripheral ring than in the center because of greater initial deposition of the larger sediment particles. The coarse sediments provide less physical resistance and the deeper accumulation allows better aeration for the stolons and this may aid the outward spread of a plant.

How *Carex lyngbyaei* establishes at the outermost limits of vegetation is unknown. It flowers and produces abundant seed every growing season, but the vitality of the seeds and the requirements for seed germination and seedling establishment are not known. Single culms of *Carex lyngbyaei* present on levees at distances of 1.8 km seaward into the tidal zone have probably developed from seed. Many apparently isolated single culms located many meters from other culms, however, are merely aerial shoots from a stolon. Low water availability seems an anomaly in a frequently flooded tidal flat, but because the fine silt and clay-sized glacial sediments pack so tightly there appears to be little available water in the sediment. Semipermanent surface cracks in the tideflat sediments may provide an invasion route for the stolons of *Carex lyngbyaei* and the halophyllic grass, alkaligrass (*Puccinellia phyrganodes*). Fine roots from the stolons extend several centimeters downward into the cracks which provide water and improved aeration. Stolons of *Potentilla egedii* are not restricted to cracks but spread horizontally across the tideflat surface in all directions. Rootlets penetrate only a few millimeters into substrate.

Culms and attached stolons of *Carex lyngbyaei* plants are frequently uprooted and transported by wave action during both the dormant and growing seasons. The vegetation at the seaward edge and its substrata are subjected to continuous disturbance.

That *Carex lyngbyaei* is best adapted to moderately saline environments is evident by its distribution on the Eyak River marsh. The absence in the Eyak River marsh of some plant species adapted to saline water, e.g., glasswort (*Salicornia*

europea) and sea blite (*Suaeda depressa*) and the low abundance of other hallophyllic taxa (*Puccinellia* spp.), and arrowgrass (*Triglochin* spp.) is indicative of its low to moderate salinity. However, long term inundation by moderately saline water, in itself, may not be limiting to survival, growth, and distribution of intertidal plants. Rather, the turbid water frequently inundating the intertidal wetlands on the Eyak River Marsh may limit photosynthesis by reducing the light that reaches the leaves and further, by covering them with silt. Windlodged live culms may be completely buried by sediment deposition, further reducing photosynthetic surface.

Secondary Succession on Post-uplift Supertidal Wetlands

A well developed sedge vegetation similar to that now present on the intertidal wetlands was present on the current supertidal area of the Eyak River Marsh prior to the uplift. Most of the foreshore levees now occupied by shrubland were almost without shrubs. Wetland meadow vegetation-types were present in interlevee basin habitats.

Four major wetland vegetation-types were present on supertidal levees: mixed herb meadow on the most seaward levees occasionally flooded by tidally lifted water; *Myrica gale* var. *tomentosa* low shrubland on inland levees infrequently flooded by tidally raised water and occasionally flooded directly by glacial meltwater in periods of excessive runoff; *Salix* spp. mid-stature shrubland on still more-inland levees above the reach of tidally lifted water and flooded occasionally by river runoff; and *Alnus crispa* ssp. *crispa* tall shrubland on the most-inland levees, flooded very occasionally by river runoff. Distinct vegetation zones of shrubland were present before the uplift. Since uplift, zonation has become much less distinct. The same three major species of shrubs have extended their distribution to the outermost levees and *Myrica gale* var. *tomentosa* now is abundant 800 m seaward in intertidal wetlands.

Succession from herbaceous vegetation to woody vegetation is a normal and natural progression on tidal wetlands. It already was taking place on the Copper River Delta wetlands prior to the earthquake uplift, but at a very slow rate. Vegetation, of course, is always dynamic. A 'stable' vegetation is one where the rate of succession is low, but succession is there, nevertheless. Succession occurs in response to the nature and combination of intrinsic and extrinsic environmental influences as controlled by the genetic potential of the component taxa. When environmental change is slow, the vegetation response is also slow. But, when a high rate environmental change occurs (e.g., the 2-3 m uplift that occurred in the Copper River Delta), the rate of succession increases.

There may be greater reciprocal positive feedback between plant and environment driving succession in tidal wetlands than in most other habitats. On a small scale, the basically geological process of levee development is enhanced by the establishment of herbaceous vegetation which, in turn, increases the rate of sediment accretion to the point where depositional rates decrease because of increased heights of the substrate surface above the level of the tide. This has, and is, taking place on the Copper River wetlands at a relatively rapid rate. Tidal meadows were present within 10 years after the uplift on tideflats where fishermen once set gillnets for salmon. Five years later, this meadow extended over a kilometer seaward and the vegetation on upper part of the inter-tidal zone had changed from herbaceous meadow to shrubland. Similar changes in the physiognomy and composition of the vegetation were taking place on the wetlands present before the uplift. These successional developments continue. Some, such as the seaward extension of sedge meadow and the spread of shrubs onto levees, proceed at slower rates. Others, such as the increase in shrubs on occasionally flooded intertidal levees and interlevee basins, proceed at faster rates—at least for awhile.

It is difficult to estimate what the rates of succession would have been if the uplift had not occurred. Since the entire delta area was uplifted, there is no control in the scientific sense. What of the future? The Copper River Delta is located in one of the most active tectonic zones on the surface of the earth. Less than 200 km east is the Yagataga Gap, one of three locations of high potential for a major earthquake on the Pacific Coast of North America. When, not if, this earthquake occurs, the Copper River Delta will be affected. What will happen to the vegetation if another uplift occurs? Probably more of the same, but in new places.

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Mount St. Helens Ten Years Later: Past Lessons and Future Promise[1]

Introduction

When Mount St. Helens erupted in 1980, an outstanding scientific opportunity was created. As a result, scientists from across the country and throughout the world came to the volcano to observe geologic and biological processes firsthand. In 1982 Congress established the Mount St. Helens National Volcanic Monument on the Gifford Pinchot National Forest in recognition of the volcano's importance as a national resource for scientific study and public appreciation of volcanic features. In the 10 years since the eruption, research at Mount St. Helens has provided an excellent baseline for tracking long-term ecosystem reassembly processes (Franklin *et al.* 1985). A wide array of disturbance intensities, varying amounts of living and dead organisms carried over from pre-eruption systems and the comparative youth and simplicity of the newly established biological system make the Monument an ideal place to pursue integrative research.

Complex Disturbance Gradient

The 1980 eruptions blew down or scorched 500 km² (200 mi²) of forest. The catastrophic failure of the volcano's summit and topographic channeling of the ensuing lateral blast produced a complex gradient of disturbance that ranged from complete scouring and burial by high temperature material in the Spirit Lake basin to the deposition of cool tephra (volcanic ash) on forests northeast of the blast zone (Lipman and Mullineaux 1981). Six principal zones of disturbance (Figure 1) extend from the most heavily disturbed surfaces closest to the volcano to the outer margins of the blast zone where disturbance was less intense and survival of plants and animals was greater.

Pyroclastic flows: On the afternoon of May 18th and during subsequent eruptions, portions of the eruptive plume collapsed and hot pumice and gases flowed from the crater and into the Spirit Lake basin. Due to extreme temperatures (700° C, 1300° F) no organisms or organic material survived.

Debris flows: A heterogeneous deposit was produced when the north side of the mountain collapsed and filled a 60 km² (20 mi²) area of the North Fork Toutle River valley to an average depth of 45 m (150 feet). Plant survival on these deposits was limited to a few individuals that sprouted from root fragments scavenged from the valley floor and swept along the surface of the deposit.

Mud flows: Floods composed of a cement-like mixture of glacial melt-water, boulders and sand-sized sediments swept down the Toutle River to the north and the Muddy River and Pine Creek to the south and east. Survival was limited to a few individuals that sprouted from roots swept along the surface of the deposit.

Tree blowdown (blast) zone: Within a 25 km (15 mi) radius north of the volcano the blast stripped away the forest canopy and knocked over, or snapped off, trees. The speed of the blast ranged from 100-300 m/sec (220-670 mph). Plant survival within the blast zone varied from patches of intact vegetation protected by snow to individual plants that resprouted from the pre-eruption soil in erosion gullies formed during the first winter following the eruption.

Scorch (standing dead tree) zone: Twenty-five kilometers (15 mi) from the volcano, the blast had slowed to the point where it no longer carried enough force to knock the trees over but remained hot enough to kill them. At this point blast energy had dissipated and it unloaded its burden of fragmented rock. The hot gases ramped upward leaving a narrow band of standing dead trees along the margins of the blast zone.

Tephra deposition: The prevailing winds carried the tephra (volcanic ash) to the northeast depositing more than 100 cm (3 feet) near the volcano and traces of ash hundreds of kilometers away. The tephra blanketed forests northeast of the mountain causing a temporary reduction in growth

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-33, 1990, Corvallis, Oregon, Mark V. Wilson and Nan C. Vance, editors.

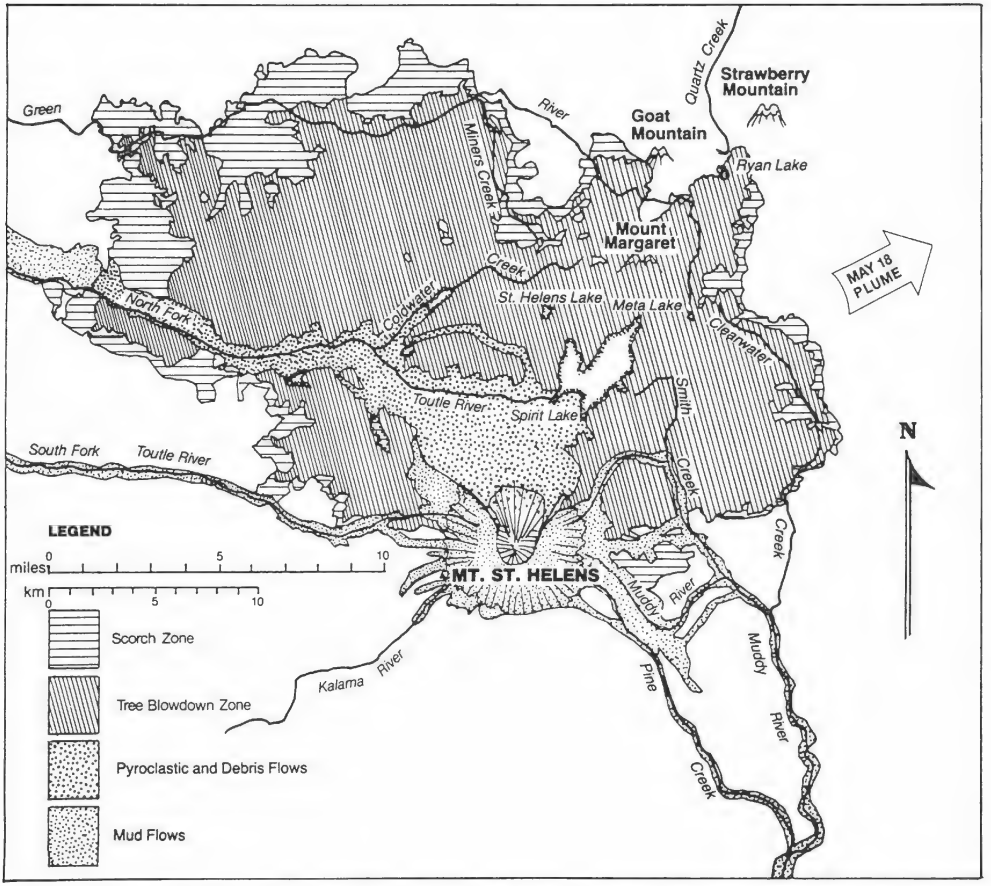

Figure 1. Zones of disturbance caused by the 1980 eruption of Mount St. Helens. In addition to the types of disturbances shown, tephra was deposited in a broad swath to the northeast of the summit.

due to damage from elevated temperatures on tephra-covered foliage. Growth recovered and in some cases, increased as the trees responded to the absence of competition from tephra-covered understory vegetation.

Research Provides Unique Insights

An impressive array of studies has documented processes of ecosystem reassembly along the large-scale gradient of disturbance. The following are studies and findings that serve as a sampling of biological research conducted at the volcano and, we hope, will entice investigators to pursue research at Mount St. Helens in the future.

Crater thermal springs: Microbiologists believe that the high nutrient, low oxygen conditions that exist in thermal springs in the crater are similar to the conditions that probably existed during the early stages of the evolution of life on earth. Dr. John Baross of the University of Washington and colleagues are sampling stream fumaroles and thermal springs to study primitive Archaen bacteria that occur only in volcanic areas and in very high temperature vents deep on the ocean floor (Baross and Hoffman 1985). Mount St. Helens is a particularly good place to study evolutionary processes because investigators have been able to study these populations from inception and track their development along temperature and chemical gradients at increasing distances from thermal sources. Baross and others hypothesize that these gradients

approximate the same changing conditions (cooling, oxygenation and dilution of nutrient concentrations) that existed in the wake of widespread volcanism millions of years ago. Biologists are able to study microbial responses along spatial gradients at Mount St. Helens approximating changes that occurred over very long time scales during the early stages of the development of life on earth.

Blast zone lakes: Dr. Cliff Dahm, University of New Mexico, and colleagues have tracked the rapid transformation of blast zone lakes from typical oligotrophic systems prior to the eruption through total anaerobiosis during the months following the eruption to near total recovery five years later (Dahm *et al.* 1982, Baross *et al.* 1982, Wissmar *et al.* 1982). The removal and virtual vaporization of forest vegetation by the blast introduced tremendous quantities of useable ammonium, carbon and other energy sources (sulfur, iron and manganese) into the lakes as rain water percolated through the shattered forest and ash deposits. Widespread oxygen depletion occurred as bacterial populations responded to increased nutrient levels. Anoxic conditions persisted for a relatively short time. Conditions rapidly returned to normal as wind and seasonal turnover stirred oxygen into water columns and available nutrients were processed by microbial activity and diluted by incoming precipitation. Dr. Richard Petersen, Portland State University, and colleagues are continuing a basic limnological survey of three blast zone lakes. An interesting aspect of their work involves a comparative study of newly formed lakes that have remained in pristine condition with those that have been stocked with fish nine years after the eruption.

Blast zone streams: Streams were adversely affected by the large quantities of sediment introduced by erosion. Large masses of sediment were washed into streams filling and chronically destabilizing stream beds and causing rapid channel changes. Dr. James Sedell, Pacific Northwest Research Station, Dr. Chuck Hawkins, Utah State University, and colleagues have determined that the rate of recovery of streams varied with the quantity of sediment introduced, steepness of stream bed and presence of large, stable logs in the stream channels (Sedell and Dahm 1983, Hawkins 1988). Where large, stable logs were left, stream beds were anchored producing a series of pools and riffles that aided the recovery of fish habitat (spawning gravels and substrates for aquatic insects upon which the fish feed). In the absence of large, woody debris fish habitat has been slow to recover. Fish that survived under ice-covered lakes have served as sources for the recolonization of blast zone streams. Anadromous (migrating) fish appear to survive their journey up the sediment-laden waters of blast zone streams to spawn in the clear waters of tributary streams (Bisson *et al.* 1988).

Blast zone vegetation: Extensive vegetation sampling across the disturbance gradient by Dr. Jerry Franklin, Pacific Northwest Research Station, Peter Frenzen, St. Helens National Volcanic Monument, and colleagues has demonstrated the importance of survivors to the recovery process (Halpern and Harmon 1983). The most conspicuous survivors were small Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) trees and huckleberry shrubs (*Vaccinium* spp.) that survived the eruption intact, bent over beneath snowbanks (Means *et al.* 1982). For non-woody species the most common means of survival was sprouting from root stocks remaining in the pre-eruption soil that was exposed by erosion or covered by deposits less than 15 cm thick (Antos and Zobel 1985). Weedy plant species such as fireweed (*Epilobium angustifolium*) and pearly everlasting (*Anaphalis margaritacea*) sprouted in areas clearcut prior to the eruption. Forest understory species survived on the upturned root masses of blowdown trees and in sheltered sites alongside stumps and under logs. In the ten years since the eruption the composition and cover of vegetation in blowdown forests has become steadily more similar to that typical of clearcuts (Halpern *et al.* 1990). Forest understory species have died back and areas have been colonized by weedy species that possess strong dispersal capabilities and a tolerance for environmental extremes.

Birds and small mammals: Through repeated population surveys, Dr. Jim MacMahon, Utah State University, Charlie Crisafulli and colleagues have documented the responses of birds and small mammals across the disturbance gradient. Ten years after the eruptions, few bird species are present in the pyroclastic flow, debris avalanche and tree blowdown zones, where vegetation recovery has been slow. The common raven (*Corvus corax*) and mountain bluebird (*Sialia currucoides*) are examples of species found in the most heavily disturbed areas. Standing dead forests harbor species such as the American robin (*Turdus*

migratorius) and hairy woodpecker (*Picoides villosus*) but lack many of the foliage-loving species found in undisturbed forests. Ashfall areas support bird life similar to undisturbed forest sites.

Of the 32 species of small mammals thought to be living near Mount St. Helens only 14 are known to have survived (Andersen and MacMahon 1985a). Species that live beneath the soil surface such as the northern pocket gopher (*Thomomys talpoides*) or hibernators such as the Pacific jumping mouse (*Zappus trinotatus*) survived where other surface dwelling or non-hibernating animals perished (MacMahon *et al.* 1990, Andersen and MacMahon 1985b). Species that have returned to the blast zone tended to be generalists having few specific habitat requirements and a broad food base (e.g. deer mouse, *Peromyscus maniculatus*, and golden-mantled ground squirrel, *Spermophilus saturatus*). Species with narrower requirements will probably not return until forest vegetation recovers and food and hiding cover are abundant.

Conclusions

Ecosystem reassembly at Mount St. Helens is a function of the carry over of living and dead organisms and the suitability of the post-disturbance habitat. The importance of biological legacies observed at Mount St. Helens has been instrumental in the development of emerging land management strategies such as New Forestry (Franklin 1989). In the years ahead, as scientists continue to monitor biotic recovery at the volcano, new information will emerge that will be invaluable to managers faced with evolving global issues such as biodiversity and conservation biology.

It is difficult to predict precisely the future structure and composition of plant and animal life at Mount St. Helens due to the uncertainty associated with the prevailing weather (e.g. incidence of recurring drought and/or flooding) or future volcanic activity. What is certain, however, is that the landscape and biota surrounding Mount St. Helens will remain in a state of continual change. Research opportunities will continue to expand as our understanding of processes of ecosystem reassembly increases. The cycle of volcanic activity followed by biotic response at Mount St. Helens has been underway for more than 40,000 years. It is likely that the cycle will be repeated many times in the future.

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Recovery of Lakes in the 1980 Blast Zone of Mount St. Helens[1, 2]

Over the past 10 years, following the catastrophic 1980 eruption of Mount St. Helens, considerable research has been conducted on altered and newly created lake ecosystems in different depositional regions of the blast zone. Scientists from numerous universities, the U.S. Forest Service, and Geological Survey have had the unique opportunity of tracking geochemical responses and biological successional patterns of microbes, plants and animals leading to the recolonization and recovery of these ecosystems. These processes occurred more rapidly than was originally expected given past reports of volcanically impacted aquatic ecosystems. This paper presents some eruption impact and recovery characteristics for an altered lake (Spirit Lake) and two newly created lakes (S.F. Castle and Coldwater Lakes) in the Mount St. Helens blast zone.

Like most Cascade Mt. lakes, historical data for Spirit Lake shows that the carbonate system provides the principal base and acid-neutralizing capacities. In such lakes, the carbonate alkalinity (CA) is the major component of the total alkalinity (TA). Other alkalinity components can occur in freshwater; for example: silicates, borates, ammonia, organic acids, sulfides, and phosphates. Usually for Cascade Mt. lakes, the concentrations of each of these non-carbonate alkalinity components are very low in comparison to the carbonate species. Prior to the 1980 eruption, values of TA (139 μq/liter), CA (136 μq/liter), pH (7.3) and dissolved organic carbon or DOC (0.8 mg/liter) of Spirit Lake waters were typical of other subalpine lakes in the Cascades (Wissmar *et al.* 1982 a,b, in press).

During the 1980 eruption, Spirit Lake was directly impacted by debris avalanches and pyroclastic flows. Spirit Lake is located 8 km NW of the crater. Two new lakes, S.F. Castle and Coldwater Lakes, were created by massive debris flows in the Toutle River valley downstream from Spirit Lake. After the eruption, TA and pH values for the three lakes ranged from 1,520 to 4,500 μq/liter and 6.2 to 6.6, respectively (Wissmar *et al.* 1982a). These values were high in comparison to other volcanically impacted lakes (Bortelson *et al.* 1977, Sigurdson 1977). In Spirit Lake, TA and DOC were 36 and 64 times pre-eruption values (Figures 1 and 2).

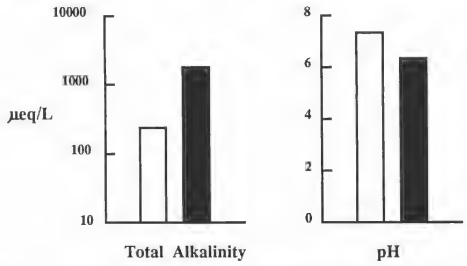

Figure 1. Total alkalinity (μq/liter) and pH in Spirit Lake before (open bars) and after (solid bars) the 1980 Mount St. Helens eruption.

The unique characteristics of the Mount St. Helens volcanic eruption and geochemistry, such as low inputs of sulfate and high loadings of organics from devastated forests to lakes, combined to form chemical environments favorable to biological activity. In contrast to many other volcanically impacted lakes, chemical environments of Mount St. Helens lakes provided considerable buffering through weathering reactions. These conditions, which initially prevented the complete destruction of microorganisms, along with the presence of adequate organic and inorganic substrates for bacterial activity (Figures 2 and 3), stimulated recovery via a succession of microbially mediated reactions.

After the eruption of Mount St. Helens, when the volcanically impacted lakes had pH values greater than 6.0, CA values along with increases in concentrations of dissolved organics suggested that organic acids contributed to the buffering system (McKnight *et al.* 1988, Wissmar *et al.* 1990). During 1980 and 1981 dissolved organic acids contributed most of the surplus alkalinity in these lakes (Figure 4). Following this period, organic acid alkalinities relative to TA declined

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-33, 1990, Corvallis, Oregon, Mark V. Wilson and Nan C. Vance, editors.

[2]Research funded in part by the National Science Foundation, U.S. Forest Service and the U.S. Army Corps Eng.

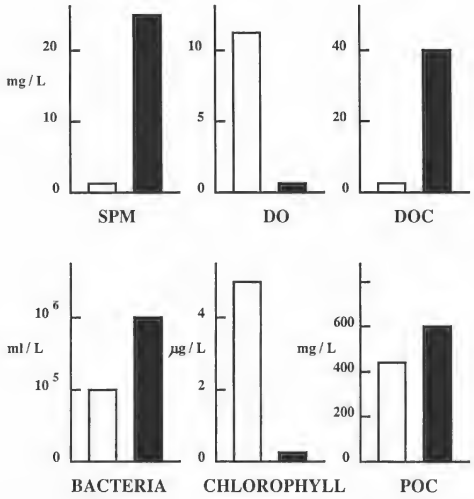

Figure 2. Selected physiochemical and biological characteristics in Spirit Lake before (open bars) and after (solid bars) the 1980 Mount St. Helens eruption. SPM = suspended particulate matter (mg/liter); DO = dissolved oxygen (mg/liter); DOC = dissolved organic carbon (mg/liter); bacteria (ml/liter); chlorophyll (µg/liter); POC = particulate organic carbon (mg/liter).

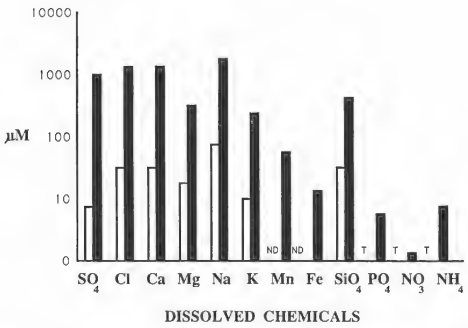

Figure 3. Selected dissolved inorganic chemical characteristics in Spirit Lake before (open bars) and after (solid bars) the 1980 Mount St. Helens eruption. All concentrations in micromoles (µM).

while CA increased. This increase in CA reflected the decrease in organic acids due to dilution by runoff waters and microbial mineralization. CA was essentially controlled by contributions of bicarbonate ions due to chemical weathering, possible anionic exchange, and microbially mediated reactions. Values for pH of surface waters of Spirit Lake from before and after the eruption (~7 years) demonstrates the rapid recovery and well-buffered conditions in the lake following the eruption (Figure 5).

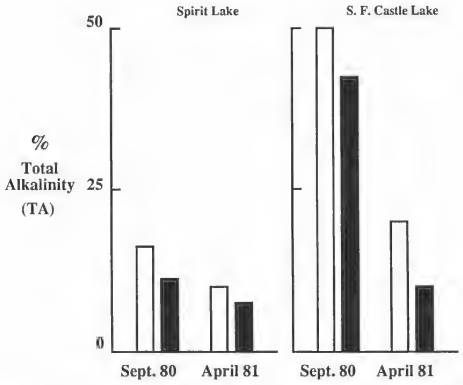

Figure 4. Comparison of surplus and organic alkalinities as percent of total alkalinity (TA) in Spirit and S.F. Castle Lakes between September 1980 and April 1981. Surplus alkalinity (open bars) represents the difference between TA and carbonate alkalinity (CA). Organic acid alkalinity (solid bars) represents the alkalinity contributed by dissolved fulvic and hydrophylic acids.

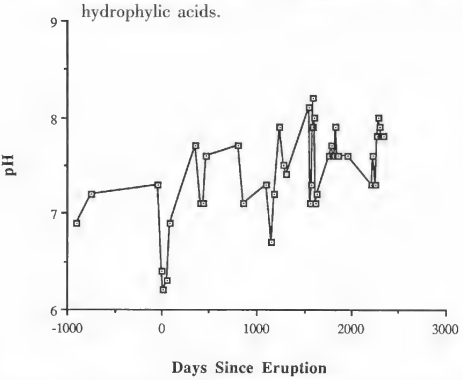

Figure 5. Changes in pH values of surface waters in Spirit Lake from before and after the 1980 Mount St. Helens eruption (~7 years).

Even though weathering, organic and microbial reactions were evidently the important processes regulating alkalinity of these lakes, patterns of changes in pH, TA and DOC (Wissmar *et al.* 1990) and changes in microbial assemblages and processes also suggested a sequence of biological reactions that occurred during the early recovery period of 1980 and 1981. For example, immediately following the eruption and high inputs of organic and inorganic materials, the lakes were relatively closed ecosystems. The sequence of reactions began with the reduction of oxygen first, then the oxidation of organic matter (Baross *et al.* 1982, Lilley *et al.* 1988). The organic reductants

supplied electrons to the lowest unoccupied level, oxygen. These reactions were accompanied by microbial reduction of nitrate (Wissmar *et al.* 1988). Other possible reactions (not measured) were most likely microbially mediated; for example, fermentation and the reduction of sulfate and carbon dioxide. The biological recovery of the lakes via succession of microbial reactions suggests a tendency for the higher energy producing reactions to dominant lesser energy producing reactions. As part of the early and later recovery processes, transient and consumer communities developed (Dahm *et al.*, in press). For example, during chemoorganotrophic phases, bacteria-zooplankton foods predominated. As turbid and high suspended particulate matter levels decreased, phytoplankton primary production increased to produce mixed bacteria-phytoplankton-zooplankton communities (Dahm *et al.*, in press).

The Mount St. Helens eruption in 1980 and post-recovery processes of the terrestrial and aquatic ecosystems are proving to be excellent situations for research, teaching and in creating public awareness of how the natural environment operates through time. The Mount St. Helens Monument and the lakes of the blast zone are truly a unique and valuable national area for acquainting the public with different environmental functions and adaptations following large-scale natural disturbance events. The evaluation of rapid changes in recovery processes of ecosystems within the Monument, now and in the future, will provide valuable insights of processes that normally structure the environment through longer term periods (centuries). These insights will prove to be useful in assessing environmental impacts of other large scale landscape changes such as fires and land clearing practices that have global implications. Such information is also valuable for increasing public awareness of man-induced and natural environmental processes that are essential to the optimal allocation of natural resources in the future. Such knowledge is also important to resource managers in developing better approaches for reconstructing damaged environments and in planning and resolving resource conflicts between different public user and environmental groups.

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The Role of Refugia in the Recolonization of Streams Devastated by the 1980 Eruption of Mount St. Helens[1]

Introduction

Streams normally consist of mosaics of habitat patches (Pringle *et al.* 1988), each of which provides conditions and resources suitable for different types of biota. We typically include riffles, pools, and runs as stream habitats, but these types of habtats can be either divided or combined dependng on the scale of interest. In fact, stream habitats can be defined at several spatial scales (Table 1). Considering the way stream environments vary at different spatial scales leads to insights regarding the factors that promote and maintain biodiversity in stream ecosystems.

In streams, environmental heterogeneity begets biological diversity. Furthermore, individual patches embedded within complex environments often act as refugia from disturbance and can strongly influence the rate of recovery in streams following disturbance. Because of the patchy nature of stream habitats, even catastrophic disturbances will seldom eliminate biota from an entire stream. Consequently, those habitat patches that are either resistant to disturbance or simply escape denudation by chance can act as sources of colonists from which disturbed habitats are subsequently recolonized. The presence of refugia can therefore confer ecological resilience to stream ecosystems as a whole.

Streams Near Mount St. Helens

The 1980 eruption of Mount St. Helens eliminated stream communities in several surrounding basins. The eruption had two primary effects on the physical environment of these streams. First, massive quantities of ash and volcanic debris entered many stream channels. Second, the upslope forest and riparian communities were destroyed or dramatically altered. Stream habitats changed in several ways as a consequence of these primary effects. Many channels became shallower and wider because of the increased sediment load. Mean particle size and substrate heterogeneity decreased as did pool frequency and depth. Summer temperature increased because of decreased shading associated with the loss of riparian vegetation.

Since the 1980 eruptions, the character of these streams has started to return to pre-eruption conditions. Most of the fine sediment has been flushed out of high-gradient streams, and these channels are now nearly identical in channel structure and substrate composition to non-impacted channels. In many low-gradient streams, scour has produced a streambed mosaic of different sediment sizes and has created deep pools around fallen trees and other resistant objects. The primary environmental differences that have remained between impacted streams and those outside the zone of devastation are those associated with the removal of vegetative cover: increased water temperature, increased production of algae, and decreased inputs of terrestrial litter. Otherwise, impacted streams offered habitats suitable for many species soon after the eruptive events that eliminated stream biota. Biota have now recolonized all of the disturbed streams in the Mount St. Helens area, although to varying degrees.

We have been studying recovery of stream biota in the Clearwater Creek basin for the last 10 years. The Clearwater basin is located just inside the blast zone approximately 10 km NE of Mount St. Helens. The basin consists of a broad alluvium-filled valley bordered by steep valley walls. The main stem of Clearwater Creek (ca. 1% gradient) receives runoff from several tributaries draining the higher gradient sub-basins. The eruption killed all of the forest and riparian vegetation surrounding tributaries draining the southwestern side of the

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TABLE 1. Examples of different kinds of refugia that may occur at different habitat spatial scales. The list is partial and meant for illustrative purposes only.

Spatial Scale	*Kind of Refugia*
Particles	Sand
	Cobbles
	Wood
	Macrophytes
Channel Unit	All of the above plus:
	Different types of particles
	Complex edges
	Different types of cover
	Water depth
	Accumulations of large wood
	Groundwater seeps
	Riparian and instream vegetation
Reach	All of the above plus:
	Different types of channel units
	Alluvial areas
	Tributaries
	Hyporheic areas
Section	All of the above plus:
	Different types of reaches
	Lentic features (e.g. oxbows)
Watershed	All of the above plus:
	Different types of sections

basin. Basins on the northeastern side of Clearwater Creek were not disturbed so completely. The upper areas of several basins were outside of the scorch-blowdown zone and had intact forest after the eruption. In other drainages, vegetation was destroyed only in small parts of their basins immediately adjacent to Clearwater Creek. The different types and intensities of disturbance within the Clearwater basin produced systems with different amounts and types of refugia. Differences in refugia among streams strongly influenced recolonization by different kinds of stream biota.

Algae

Ash scoured and filled stream beds and removed all measurable algae from many stream channels. One year after the eruption algal standing crops varied significantly among disturbed streams. Some streams had algal standing crops that were indistinguishable from undisturbed control sites, whereas other sites had not recovered significantly (S. V. Gregory and C. P. Hawkins, unpubl. data).

For algae, the specific location of refugia and their proximity to disturbed reaches within a basin were probably not significant with respect to patterns and rates of recovery. The small size of algal cells make them extremely rapid, passive (e.g. via wind or currents) dispersers from either within or outside basins. Recovery of algal community composition and production appears to be largely controlled by the substrate and temperature conditions present at a site (Steinman and Lamberti 1988, Aumen *et al.* 1990). The different rates of recovery observed among sites were a function of the inherent rapid dispersal capabilities of algal cells and the different rates of re-exposure of stable substrates within each stream.

Invertebrates

Recovery of invertebrate assemblages has also varied significantly among streams. Five years after the eruption, streams in minimally disturbed basins where the forest remained intact had more taxa and greater diversity than basins which had either partial or no forest remaining (Hawkins 1988). Streams with forests remaining in the headwaters had more taxa than basins in which all of the forest was destroyed. Composition of the communities in the streams appeared to be largely a function of differences in temperature and random colonization. Because trophic guild structure was similar among sites, differences in the type of food sources present among streams did not appear to be important.

The reasons for the differences in taxonomic richness among sites appears to be a function of proximity of sampled reaches to refugia habitats. The location of these refugia correspond to the location of intact forests within basins. The most recognizable modes of dispersal out of these refugia are passive displacement of individuals by stream currents and active aerial flight by adults.

Amphibians

Densities of tailed frog tadpoles (*Ascaphus truei*) showed a pattern among streams slightly different than that observed for invertebrate taxonomic richness (Hawkins *et al.* 1988). Highest densities were found in basins that were partially deforested. Lowest densities were observed in basins that were completely deforested, and intermediate densities occurred in basins that were minimally disturbed.

For this species, the presence of heavy forest shade appears to be a critical habitat component that served as a refuge. Adult survival and

reproduction seem to require the cool, moist conditions that a dense forest canopy provides. Tadpoles are less restricted in their use of habitats. In fact, as long as stream temperatures are below about 18° C, tadpoles thrive under open canopies with high amounts of algae, their primary food. The reason tadpole abundances were highest in the partially deforested basins is probably because these basins provided near optimal conditions for both adults and tadpoles. In the other types of basins, either suitable adult habitat was absent or food for tadpoles was low.

The eventual recolonization of heavily disturbed basins, in which this species is locally extinct, will depend on both re-establishing conditions suitable to adults and the dispersal abilities of potential migrants. Although downstream dispersal by tadpoles within a basin can be rapid, movement into neighboring basins will probably be slow because adult tailed frogs are poor dispersers. For isolated basins near the volcano, recolonization may take 100 yr or more because of the combination of distance to nearest refuge and slow dispersal rates.

Fish

Prior to the eruption, Clearwater Creek contained high densities of brook trout (*Salvilinus fontalis*), cutthroat trout (*Onchorhynchus clarkii*), and shorthead sculpin (*Cottus confusus*). Immediately following the eruption, these populations had been eliminated or nearly so. Since the eruption, densities of these three species have steadily increased. By 1988, total trout densities were about 1/10 that of typical densities in small Northwest streams. In contrast, by 1985 sculpin populations had reached densities comparable to, or higher than, populations in nearby undisturbed streams. Recovery of fish populations in this stream was completely dependent on the existence of refugia within the basin, because a 30 m waterfall blocked any migration from downstream sources.

For brook trout, the primary refugia were headwater lakes. At the time of the eruption, these lakes were covered with an ice layer that insulated them from the volcano's heat. In addition, these lakes did not experience the destructive scour associated with downstream transport of deposited ash. We have observed hundreds of brook trout moving out of Meta Lake and into the upper reaches of Clearwater Creek. Several springs occur along Clearwater Creek and may also have served as refuge sites. The springs are off the main channel and would not have experienced the scour that affected most of the stream. As of 1988, the stream bed was still too unstable to provide suitable spawning areas for brook trout. Brook trout are autumn spawners and the eggs that are deposited are almost certainly destroyed by the scour and fill that occurs during winter storms. The size structure of the brook trout population in Clearwater Creek also indicates that individuals in the stream originated from somewhere outside the stream. The population is dominated by two-year and older fish. We have observed very few young-of-year or one-year-old brook trout.

It is unclear what areas served as refugia for cutthroat trout, but they probably occurred within the stream. Cutthroats are known to be stream spawners, and no cutthroats were observed either in or leaving Meta Lake. The few cutthroats that remained after the eruption probably survived by seeking protection among large, stable pieces of woody debris. Their currently low numbers are likely due to poor spawning success associated with the instability of stream substrates. We have observed more young-of-year cutthroat than brook trout in Clearwater Creek indicating that cutthroats are more successful at spawning within the stream than are brooks. The most likely reason for this is that cutthroats spawn in spring after most of the destructive floods have occurred.

The rapid recovery of sculpin populations is difficult to explain. Because sculpins are benthic fish, they should presumably be more sensitive to scour than water column species like trout. We have found that shorthead sculpins are habitat generalists and occupy almost all areas of the stream bottom including riffles and pools and a wide range of substrates spanning sand to cobble. Any habitat patch that escaped destruction could therefore have served as a refuge and source of colonists. This species also spawns in the spring, thereby avoiding the potentially most destructive floods. Furthermore, emerging sculpin larvae appear to prefer shallow, sandy reaches with dense algal growths and high populations of midge larvae. The eruption actually increased the abundance of these types of patches, thereby facilitating survivorship of young individuals. In contrast to both species of trout, the age structure of the sculpin population is more normal and skewed toward younger fish.

Conclusions

Population and community recovery following disturbance depends on the presence of refugia and dispersal mechanisms that allow individuals in one patch to move to another patch. Successful recovery also depends on the overall environment returning to a set of conditions that allow species survival. In our examples, we have illustrated that refugia, dispersal ability, and suitable conditions are to some extent species-specific. The trajectories of overall community recovery in the disturbed streams near Mount St. Helens will therefore depend on several factors: (1) the type of habitats surviving, (2) the mix of species within those habitats that can act as colonists, (3) the dispersal abilities of individual species, and (4) the degree to which and (5) length of time it takes different stream environments to return to stable conditions.

Acknowledgements

The work on which this paper is based was supported in part by National Science Foundation grants BSR-841627 to CPH, BSR-8414325 and BSR-8508356 to Oregon State University, and funds from the PNW Experiment Station Anadromous Fish Habitat Project (U.S. Forest Service). We thank Nan Vance for her patience, good humor, and constructive editing.

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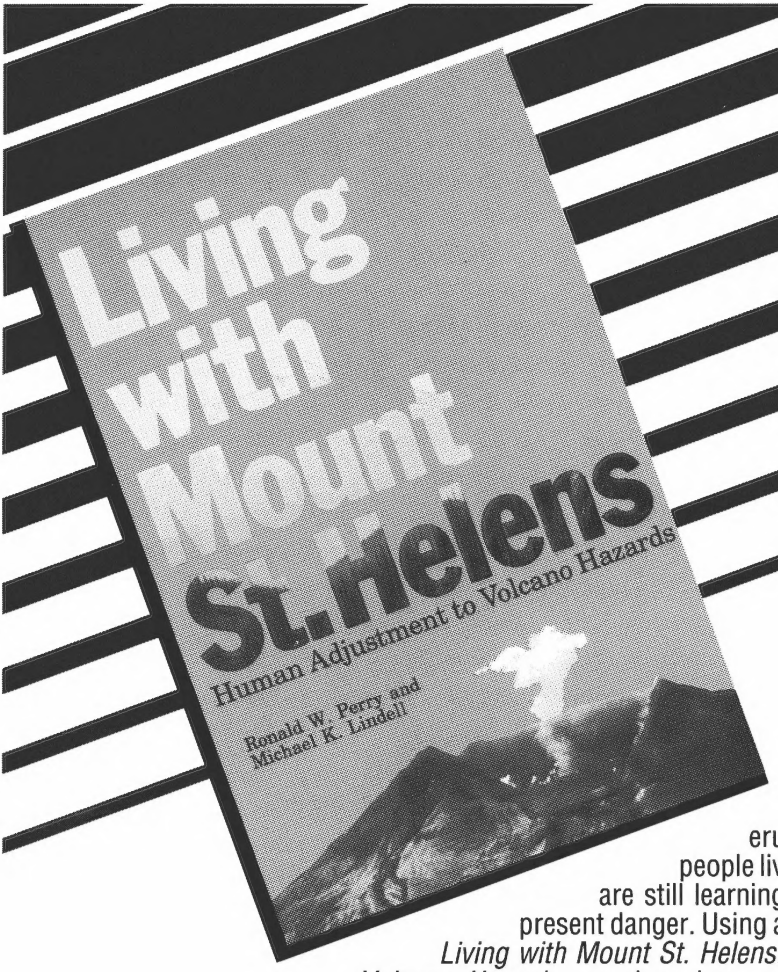

A decade after the May 18, 1990, eruption of Mt. St. Helens, people living close to the volcano are still learning to cope with its ever-present danger. Using a sociological approach, *Living with Mount St. Helens: Human Adjustment to Volcano Hazards* examines how residents of Toutle and Lexington, Washington, have responded to the catastrophe.

Employing statistical surveys, personal interviews, and a review of hazard management literature, Perry and Lindell analyze and interpret the ways residents reacted during and after the eruption. Their work contains valuable information for emergency managers who wish to inform, educate, and protect the general public from danger.

Ronald W. Perry is professor of public affairs and director of the Public Administration Program at Arizona State University. Michael K. Lindell is associate professor of psychology at Michigan State University.

Index, bibliography, illustrations, 6" x 9", 220 pages. Paperback, ISBN 0-87422-053-X, $20.00. If ordering, please add $2.00 for shipping and handling, and 7.5% sales tax if a resident of Washington.

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